The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England

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Synopsis

Over 400 Lower Liassic insect fossils collected in Dorset, England, have been studied. These include 66 species in over 30 genera of which 11 new genera and 21 new species are described and their relationships discussed. Several families of insects are recorded for the first time in Britain, while the Orders Dermaptera (earwigs), Phasmatodea (stick-insects) and a scale-covered lepidopterous insect are recorded for the first time in the Lower Lias.

The following new taxa are proposed: *Nannoblattina petulantia* sp. nov. (Blattodea); *Brevicula gradus* gen. et sp. nov. (Dermaptera); *Liassophlebia pseudomagnifica* sp. nov., *Hypsothemis fraseri* sp. nov. and *Dorsettia laeta* gen. et sp. nov. (Odonata); *Archelcana durnovaria* sp. nov., *Orichalcum ornatum* gen. et sp. nov., *Regiata scutra* gen. et sp. nov. and *Micromacula gracilis* gen. et sp. nov. (Orthoptera); *Durnovaria parallela* gen. et sp. nov. (Phasmatodea); *Paraprosbole rotruda* gen. et sp. nov. and *Mesocixiella* (?) *fennahi* sp. nov. (Hemiptera–Homoptera); *Metaraphidia confusa* gen. et sp. nov. and *Priscaenigma obtusa* gen. et sp. nov. (Raphidioptera); *Orthophlebia capillata* sp. nov. and *Pseudopolycentropus prolatipennis* sp. nov. (Mecoptera); *Prodocidia spectra* gen. et sp. nov. (Diptera); *Archaeolepis mane* gen. et sp. nov. of new family Archaeolepidae (Lepidoptera); *Elaterophanes regius* sp. nov., *Liassocupes* (?) *maculatus* sp. nov. and *L.* (?) *giganteus* sp. nov. (Coleoptera). Eight new species of Hemiptera–Heteroptera are placed in open nomenclature.

A survey of the fauna is used to consider the environment from which the insects were derived. The Dorset insects are compared with other British and continental Mesozoic insect faunas. The palaeogeography of the Sinemurian (Lower Lias) of south-west Britain is considered and a new assessment of the distribution of the land masses is postulated based on the data derived from the fossil insects.

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Introduction

> *The complete description of the* [*insect*] *fauna from Charmouth will require considerable time, partly because the poor state of preservation imposes a heavy strain on the eyes of the investigator, and partly because the fragments require large-scale comparison with more complete material from a great variety of insect orders.* F. E. Zeuner (1962: 160)

Fossil insects are particularly well represented in the British Jurassic and were extensively collected by the Rev. P. B. Brodie who published his classic work, *The History of the Fossil Insects in the Secondary Rocks of England*, in 1845. Various authors on the continent of Europe (Giebel 1856, Handlirsch 1906–08) or in North America (Scudder 1886) have described insects from the British Mesozoic.

The present study is based almost entirely on a remarkable collection of insect fossils from the Dorset Lias made by James Frederick Jackson (1894–1966). His collection was purchased over a period of years by the British Museum (Natural History) (Zeuner 1962: 155). Jackson first published on Dorset coastal geology in 1926 but his other published works dealt only with the geology of the Isle of Wight (Lang 1968). When, in 1951, Jackson moved to Charmouth (Dorset) he spent his retirement collecting fossils in the Lower Lias, not only insects but also ammonites, crinoids and other groups, all of which came to the Museum.

Gardiner (1961) was the first to publish a description of an insect from the Dorset Lias, which was discovered in the orbit of the eye of a fossil fish during its acid preparation.

Jackson's collection of fossil insects, which consists of 434 specimens, has however not previously been studied in its entirety. Some were published by Zeuner (1962), who studied 65 specimens from the collection, 43 of which belonged to one species of Coleoptera. Two other specimens from the Dorset Lias are also included in the present study, a snakefly (Raphidioptera) in the collection of the British Geological Survey and a waterbug (Hemiptera–Heteroptera) in that of the Bristol Museum and Art Gallery.

The study of these Dorset Lias fossils is part of a wider project on British Mesozoic insects. Many of the previously-described insect fossils from British localities are the types of genera, few have been studied since they were first described and many, with new techniques, can be developed further to reveal important characters not visible when they were originally examined.

When the Jackson collection was originally received at the Museum all the specimens were given register numbers as insect fossils. Some, however, on closer examination have proved to be fragments of plants or fish. When Zeuner studied the collection there were 434 specimens registered as insects and he based his percentages of the various orders (1962: 158) on this total. In fact 30 of the registered specimens are not insects and this was taken into account when the figures were calculated for the comparison in Table 1, in which the corrected figures more accurately reflect the fossil fauna. The main discrepancies are in the Hemiptera, where Zeuner's figure for the total was too low, probably because he included some of them in his category 'cannot be classified without further detailed work', and the same is probably true of his figure for the Panorpoid complex, in which he included the Diptera, Mecoptera, and Neuroptera (i.e. Raphidioptera herein), but here the discrepancy is smaller.

Whilst all the insect orders present greater or lesser problems of identification and interpretation, the problem of identification of the Coleoptera has proved intractable (p. 164). Beetles form over 39% of the total insects and this high percentage reflects not only their persistence as fossils but also gives an indication of their original abundance. It is almost impossible to classify isolated Mesozoic beetle elytra to Recent families, because of the virtual absence of wing venation, which is used for identification in many insect groups especially amongst fossils, although in some cases a reasonable guess can be made. But when more detailed studies of Mesozoic beetles have been made, it may be possible to build up a closer association with Recent families similar to the one developed by Coope (e.g. Coope 1979) for Pleistocene beetles. In the present study a few readily recognizable and more complete beetle fossils are associated with Recent families, the rest being placed in numbered species-groups consisting of similar and probably related insects associated by size, shape and sculpturing of the elytra. This allows a rough estimate to be made of the diversity of the beetle fauna.

Table 1 Numbers of insects in Jackson collection, and percentages of each order. A – number of specimens in Jackson collection. B – percentage. C – insects from other collections included in the present study. D – Zeuner's (1962) estimate, with corrected percentage figures (a, Hemiptera; b, 'Panorpoid complex', see p. 108). Zeuner's figures have been corrected for the actual insect total and these should be used with his 1962 paper. The total number of registered specimens in the Jackson collection is 434.

	A	B	C	D
Blattodea	6	1·5	–	1·9
Dermaptera	2	0·5	–	–
Odonata	10	2·5	–	2·7
Orthoptera	83	20·6	–	22·3
Phasmatodea	1	0·2	–	–
Homoptera	5	1·2	–	2·7^{a}
Heteroptera	29	7·2	1	
Raphidioptera	1	0·2	1	3·4^{b}
Mecoptera	15	3·7	–	
Diptera	1	0·2	–	
Lepidoptera	1	0·2	–	–
Coleoptera	160	39·6	–	40·9
Indeterminate insects	90	22·5	–	26·1
Total insects	404		2	
Non-insect fragments	30		–	

Zeuner (1962: 159) mentioned a 'solitary Hymenopteron (*sic*) of the sawfly type' in the Jackson collection but does not elaborate on this statement. In spite of careful examination this specimen has not been found: in fact no Hymenoptera were found amongst the 404 insect specimens in the Jackson collection.

The descriptions of the Dorset Hemiptera–Heteroptera will be included in a joint publication on British Mesozoic Heteroptera by W. R. Dolling (British Museum (Natural History)), Y. A. Popov (Institute of Palaeontology, Moscow) and the author. This was to have been published before the present study but has been delayed; only a summary of the Dorset Heteroptera is included here.

Although many of the insects are well preserved, or represent an extension of our knowledge of the Order in distribution or time, probably one of the most remarkable fossils is the *Archaeolepis* (p. 159), showing the preservation of wing-scales very similar to those on the wings of Recent Lepidoptera.

Apart from the information afforded on morphology and the earlier occurrence of many groups than was previously known, the results of this study can be used to interpret the position of land masses in the Jurassic. Information about the extensive terrestrial fauna can also be used to evaluate the possible plant communities on the land from which the insects were derived.

Geology, preservation and techniques

Davis (1956, reprinted 1970) gave a general account of the geology of the Dorset coast; details of the rocks from which the fossil insects were obtained were given by Lang, Spath & Richardson (1923) and Lang & Spath (1926). A recent account of the zonation and correlation of these rocks can be found in Cope *et al.* (1981: 35, fig. 5a).

The insect fossils were mostly collected from the calcareous Flatstones and the Woodstone (parts of bed 83) in the Obtusum Zone (Upper Sinemurian); a few were found in the older

Turneri Zone in the Birchi Nodules (bed 75a, Lower Sinemurian). All are from a relatively short stretch of cliff at Charmouth, Dorset. Many are associated with ammonites (Figs 18, 27, 45) and four species of ammonites and four fish were mentioned by Zeuner (1962). Some of the insects are so closely associated with the ammonites that they must have been buried at the same time, in fact the wing of one of the dragonflies is literally wrapped around an ammonite (Fig. 8; p. 123). Fish remains are fairly common, although mostly very fragmentary. Few specimens have been found immediately associated with the insect fossils; the classic exception is the beetle *Elaterina liassica* Gardiner which was found in the eye orbit of a fish fossil during acid preparation (p. 164). Fragmentary plant remains are common, although the only close association of plants and insects is in the Woodstone where the insects appear to have been trapped by mud accumulated alongside the wood before fossilization.

The calcareous mudstone in which the insects are preserved varies in fineness and is frequently full of burrows made by organisms when the mud was still wet. The preservation varies from almost complete insects to isolated body sclerites or fragments of wings. Often very fine detail shows clearly as, for example, the fine hairs on the Orthophlebiidae (Fig. 48b). The hairs are usually not preserved as surface features but are preserved in the rock matrix and show up most clearly when the rock is wet and the surface refraction minimized. Some of the fossils show remains of cuticle, which shows up clearly when the specimen is wet. A few are preserved as impressions which show up more clearly in relief with strong lateral lighting.

The majority of the specimens are represented by single wings, and in a few cases the wings are broken, suggesting that they were subject to considerable tearing forces before fossilization. Differences in the original nature of the wings show up significantly in the deposit as differences in preservation. The toughened elytra of the beetles are more frequently preserved while their delicate and membranous hindwings are rare in the Dorset Lias. Curiously enough there are more pairs of beetle elytra preserved together than pairs of forewings of any other Order, even in the Orthoptera where the forewings are often thicker. In the Dorset rocks at least 40% of the Coleoptera are represented by paired left and right elytra, whereas in the Orthoptera both forewings are preserved in less than 8% of the specimens. The small, tough, beetle elytra were evidently less subject to dispersal than the larger Orthoptera forewings. In the Hemiptera, where the forewings of the Heteroptera are thicker, in only 12% of the fossils were the forewing and part of the body associated. In cockroaches, which have a more sclerotized forewing, only six specimens were found and each was represented by a single forewing.

There is no evidence of a concentration of insect fossils in the Flatstones and with few exceptions the fossil insects were well separated, occurring in separate blocks found scattered along some two miles of coastline. Thus although the zonal location of the blocks may be known there is no information on the *in situ* location of the fossils in the cliff face. The Jackson Collection was made over a period of many years.

The specimens were further developed (where possible) by degagement (removal of overlying rock) with a fine pneumatic hammer-drill and then studied with the surface of the rock dry, with lateral illumination from twin fibre optics, and with the surface wetted with 80% alcohol. The latter frequently enhances the appearance of the sclerotized parts and by cutting down the surface refraction permitted even fine hairs to be seen. Photographs were taken with the specimens both wet and dry. The scanning electron microscope was used to study fine details of surface features; while this was successful in some cases (Fig. 58d) it did not work where the features proved to be just below the surface. In the latter case the features could be seen when the surface was wet or by the use of episcopic illumination with ultra-violet light.

Check-list of insects from the Dorset Lias

Blattodea	*Nannoblattina petulantia* sp. nov.	114
	Rhipidoblattina sp. indet.	116
Dermaptera	*Brevicula gradus* gen. et sp. nov.	117
Odonata	*Liassophlebia pseudomagnifica* sp. nov.	120
	L. jacksoni Zeuner	121

Survey of the Insect Orders in the Dorset Lias

There are eleven orders of insects represented in the Jackson Collection. Orders which are known from the Jurassic or earlier, but which are not represented in the collection, are the Trichoptera, Neuroptera, Ephemeroptera and Hymenoptera. No larval stages of terrestrial or aquatic insects were found.

The best hypothesis for the derivation of the fauna is that, although the land was not far away from the marine site of fossilization (p. 183), there was no direct access to it from a freshwater site.

Blattodea. Unlike many Mesozoic faunas, cockroaches are poorly represented and only six specimens were found. Their affinities are with the many other species found in the British Purbeck and Lias formations and were representatives of widespread genera. The six specimens are placed in two species.

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* Descriptions of Mesozoic Heteroptera by Dolling, Popov & Whalley are in press.

Dermaptera. Previously the earliest earwigs known were from the Upper Jurassic of the U.S.S.R. The two specimens of a single species are the earliest representatives of the order.

Odonata. There are seven species of dragonflies in the fauna. Their affinities are in the main with species from the European Jurassic at the generic level. At the species level, most were peculiar to the Dorset fauna and indicate a different ecological origin from the rest of the British Lias. All the species are placed in extinct families and their relationship with the two extant species currently placed in the same suborder, Anisozygoptera, is not clear; they look like specialized side-branches from the main Anisozygoptera stem. *Dorsettia laeta* sp. nov. (p. 125), which shows sexual dimorphism of the wings, is the earliest example of this in the Odonata. No nymphal forms have been found.

Orthoptera. Eight species of bush-cricket and true cricket are described; some, like *Protohagla langi* Zeuner, were very large insects with a wingspan of 150 mm. Although most of the species show a generic similarity to species described from the Russian Jurassic, no doubt in part because this is the most thoroughly studied, two species, *Protogryllus magnus* Zeuner and *Locustopsis spectabilis* Zeuner, have also been found in the older Planorbis Zone of the Lower Lias of Warwickshire and Worcestershire. The family Triassomantidae (p. 129) has not previously been recorded in Britain. Judged from the number of specimens of some of the crickets, they were fairly common in the fauna from which they were derived and had structures which, in Recent species, are responsible for sound production. This suggests that sound played an important part in their communication, as in present-day crickets. The family Bintoniellidae, abundant in other Lower Lias deposits in Britain (Whalley 1982), are absent from the Dorset fauna, further strengthening the case that the ecological origin of the fauna differed from that of other British Liassic deposits.

Phasmatodea. Only a single specimen of this order was found, the first example in Britain; it is placed in the extinct family Aerophasmatidae. Recent species of the order are mainly tropical or subtropical.

Hemiptera–Homoptera. Six specimens were found but their preservation in most cases is poor. The Tettigarctid cicadas are typical of many other Mesozoic faunas where they were evidently fairly common, in contrast to the Recent fauna where only two extant species are known. The fulgoroid family Cixiidae is known from the Permian and one new species is here described from Dorset.

Hemiptera–Heteroptera. Thirty specimens were found, forming a fairly high proportion of the fauna. These specimens belong to five families, two of which will be described in a forthcoming paper (Dolling *et al.*, in press). All the landbugs belong to extinct families whereas the waterbugs can be placed in Recent families, a conclusion similar to that of Popov & Wootton (1977) in their study of the Upper Lias of Germany.

A well-preserved belostomatid waterbug (p. 146), which is broadly similar to Recent species, differs in the form of the tarsi. In Recent species these are fused to the tibia and form a unified grasping structure whereas in the Liassic fossil the tibia and tarsi are not fused and therefore a slightly different method of grasping the prey must have been used. In a number of the fossil Heteroptera, particularly conspicuous in this belostomatid, there is a reddish patch in exactly the same position as the metasternal gland of Recent species—which is also red in colour (Fig. 42, arrowed). The gland is characteristic of Recent Heteroptera and has not previously been reported in fossils. In the fossil the 'contents' of the gland are now calcitic but a preliminary analysis of the red material shows that it has a 12% sulphur content.

Raphidioptera. There are relatively few extant species of this order and there are clear indications from the fossil record that it was commoner and more diverse in the Mesozoic. Both the species described are placed in one of the extinct families.

Mecoptera. These are fairly common in the Dorset Lias and are represented by three species, all belonging to extinct families. Two are species of Orthophlebiidae which are common in Liassic deposits in Britain and elsewhere. The third species belongs to one of the more enigmatic fossil families in the Mecoptera, the Pseudopolycentropodidae, previously known only from the Upper Jurassic of continental Europe and Asia. The wings of species in this family are a very characteristic shape, differing from the widespread orthophlebiids which tend to have a more elongate, rounded wing (p. 155). The change in shape of the wing of the pseudopolycentropodids has brought about a change in the shape of the median cell and a realignment of the veins bordering this, presumably to increase the strength of the more triangular wing.

Diptera. Although two specimens are known from the Dorset Lias (p. 157), only one is clearly recognizable and it is provisionally placed in one of the Recent families of Fungus-gnats (Mycetophilidae). The Fungus-gnats of the Superfamily Bibionomorpha, to which the Jurassic specimen is assigned, are known from the Trias and Jurassic of the U.S.S.R. but are not common in the fossil record, although these delicate insects are widespread and abundant today.

Lepidoptera. The small, scale-covered, insect wing from the Dorset Lias is one of the more unexpected, and at the same time enigmatic, discoveries. There is insufficient data from the specimen to be certain of its taxonomic position within the Lepidoptera.

Coleoptera. Beetles are the most abundant and diverse of the fossils in the Dorset Lias, and while this reflects the actual diversity of beetles in the Mesozoic, it is also the result of their natural toughness and resistance to mechanical disintegration. The click-beetles (Elateridae) are the earliest known, and the preservation of the peg-mechanism on the base of the prothorax and mesothorax shows that these Jurassic forms functioned in a similar way to Recent species. The similarity of the fossil to Recent species is such that it can be placed in the Recent family Elateridae.

The Dorset cupedid beetles have elytral patterns typical of the group, which was abundant and diverse in the Mesozoic although there are few living species.

Probably the most enigmatic fossil beetles are the species of *Holcoptera*. These are common fossils in the British Lias and Upper Trias but are not known from any other part of the world. They are very distinct, with characteristic black-and-white stripes (Figs 82–87), but because little is known of parts other than the elytra it has not been possible to assign them to a Recent family. They have some general similarities to Recent *Julodis* (Buprestidae), but as yet other structural details for comparison have not been found. They are so distinctive that they may well prove to be useful as stratigraphic indicators.

Systematic section

In the following descriptions, all the specimens listed under 'Other material' are excluded from the type series. All numbers given are BM(NH) register numbers, unless otherwise stated.

Order **BLATTODEA**, cockroaches

There are still many problems in the classification of the Blattodea, because taxonomists do not agree on the major divisions of the group. Vishnyakova (1968) placed some of the Mesozoic cockroaches in the Blattidae, a family currently in use for Recent species. In the classification adopted here I do not associate the Recent and Mesozoic species in the same family but follow Fujiyama (1973), who raised the subfamily Mesoblattininae to family status. He included in the family Mesoblattinidae all the species Vishnyakova (1968) and Rohdendorf (1962) placed in the subfamily, and this classification is also followed in a study of Lower Cretaceous insects (Whalley & Jarzembowski 1985: 387). The family Blattidae is retained for geologically Recent and extant species.

Over 50 species of cockroaches, placed in 20 genera, have been described from the Jurassic rocks of Britain. Nearly half of these were considered *incertae sedis* by Handlirsch (1906), while others have been transferred to different orders (e.g. *Pterinoblattina intermixta* from Blattodea to Neuroptera). Cockroaches usually form a high percentage of fossil insect faunas (Fujiyama 1973), but in the Dorset Lias there are only six specimens out of more than 400 insect fossils.

The classification of Mesozoic cockroaches is based mainly on wing venation. Many of the wings, described as distinct species, have only very small differences of venation. In Recent cockroaches the forewing venation may vary considerably between specimens of the same species, but until the work of Vishnyakova (1964) intraspecific variation had not been considered in Mesozoic species. Vishnyakova considered that only the median vein was relatively constant and that some of the specific diagnoses previously based on venation differences were probably only intraspecific variation.

Two types of forewing were found in the Lias which are considered here as distinct species. One species has a rather narrow and heavily sclerotized forewing with a strongly curved costal margin (*Rhipidoblattina*), while the other is larger and broader. The possibility was considered that these wings represented one sexually dimorphic species. However, in sexually dimorphic Recent species the forewing of the female is usually shorter, broader and more rounded than in the male, while in the fossils the more rounded wing is much larger than the other. Since there are other differences in the venation of the anal area and in the curvature of the cubital vein, the two types of wing are regarded as distinct species. The Dorset cockroaches, which are from the Obtusum Zone, are different from cockroaches described from the older Planorbis Zone from the west Midlands.

Family **MESOBLATTINIDAE** Handlirsch, 1906

Subfamily **MESOBLATTININAE** Handlirsch, 1906

The subcostal area of the forewing is small and the subcostal vein cannot usually be distinguished. Upper Carboniferous – Upper Jurassic. Cosmopolitan.

Genus *NANNOBLATTINA* Scudder, 1886

[Scudder 1886: 475, 1890: 376; Handlirsch 1906: 533]

Type species. *Nannoblattina prestwichi* Scudder 1886: 475, here designated. Jurassic, Europe.

Diagnosis. R and M fused for part of their length in the forewing.

Remarks. Although there are several species of *Blattula* Handlirsch in which R and M are joined (Vishnyakova 1968), in other Mesozoic cockroaches these veins are separate. Species of *Blattula* where R and M are joined are much smaller than *Nannoblattina*. No type-species designation has hitherto been made for this genus, which has three included species: I have selected as type the species with the most complete type specimen.

Nannoblattina petulantia sp. nov.

Fig. 1a, b

Diagnosis. As genus; anal veins angled.

Name. 'Capriciousness'.

Description. Forewings, subcostal vein unbranched, subcostal area small. R with parallel branches, some basal and apical ones forked, running to costal margin. Intercalary veins present. M with two main branches off MA, with at least two further branches off each of these. Base of M obscured, possibly joining R near centre of wing but may run contiguously all along R to base. Cu strongly curved, clearly separate from base of R + M, branches from Cu curved forward. Anal area reticulate, some of the veins branched near the margin.

Holotype. In.53929; Flatstones, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: length 16·3 mm; width 8·3 mm; anal area 9·4 × 4·5 mm.

Other material. In.51004.

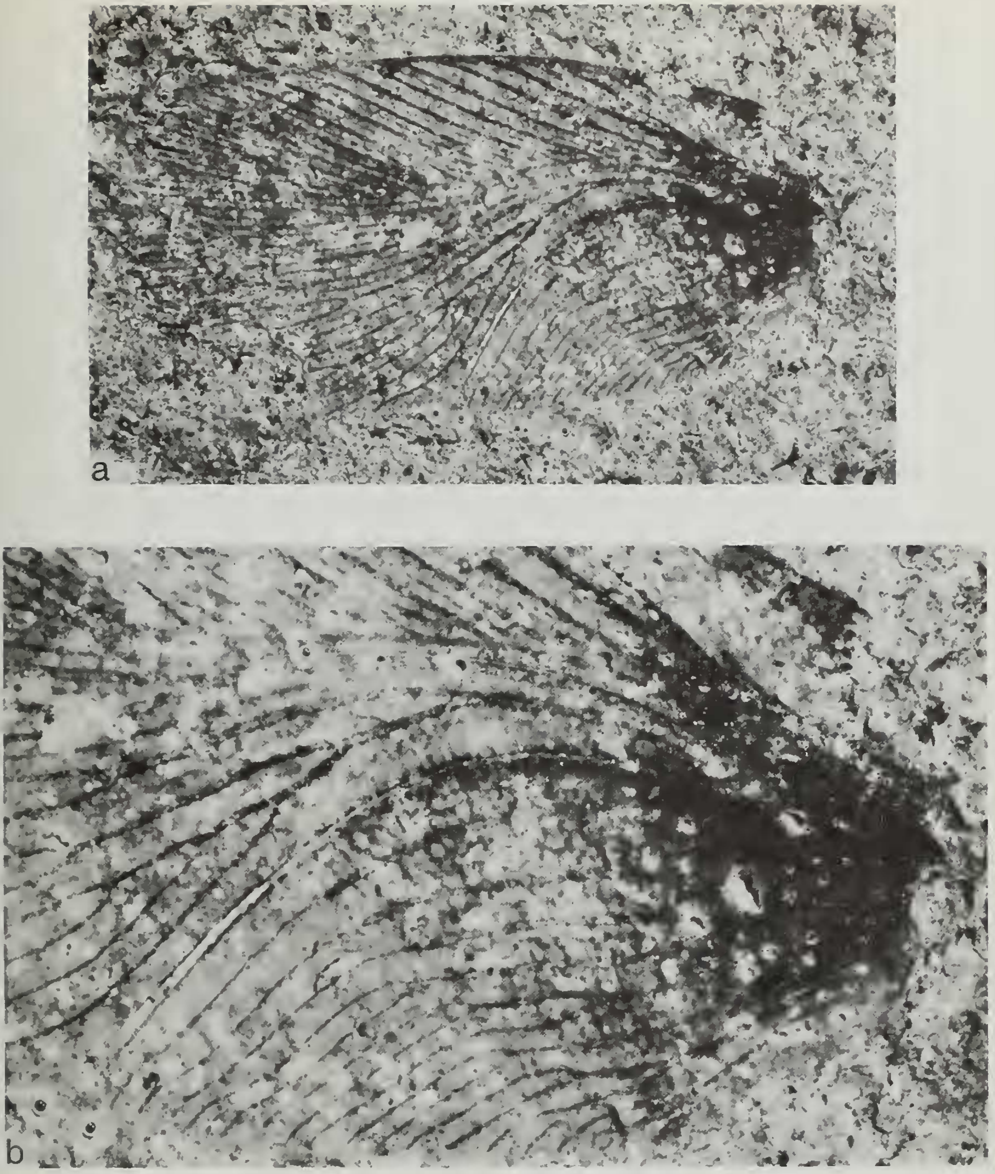


Fig. 1 *Nannoblattina petulantia* sp. nov. (Blattodea). **Holotype**, In.53929. a, forewing, 16·3 mm long. b, forewing, venation of anal area.

Discussion. The second specimen In.51004, although basically similar to the holotype, has a narrower anal area and the cubital vein, while curved, does not dip down as sharply as in the holotype. There is, in the holotype specimen, a trace of a vein close to the radius which might be the base of the medial vein, but even just anterior to the centre of the wing it appears to fuse with the radius. The shape of the anal area, the arrangements of these veins and the curved posterior branches of the cubital are characteristic of this species. It is much larger than the other species of *Nannoblattina* previously described from the British Lias or Purbeck beds.

Genus *RHIPIDOBLATTINA* Handlirsch, 1906
Fig. 2

Type species. *Mesoblattina geikiei* Scudder, 1890, by monotypy.

The remaining four specimens of Mesoblattininae from the Dorset Lias are incomplete and cannot be more closely identified. They are all basically similar and have slender forewings with a strongly curved costal margin that is heavily sclerotized, and a rather truncated anal area. The radial vein is gently curved but the details of the rest of the wing are not preserved. On the evidence available they are only provisionally placed in *Rhipidoblattina* (Handlirsch 1906: 531).

Material examined. In.49212; In.49249; In.53909; In.53920 (Fig. 2).

Dimensions. 14 mm (estimated complete wing length, under 15 mm).

Fig. 2 *Rhipidoblattina* sp. (Blattodea). In.53920, forewing, 14 mm long.

Order DERMAPTERA, earwigs

The earliest earwigs previously known are from the Upper Jurassic of the U.S.S.R. The two specimens from Dorset differ from Recent Dermaptera mainly in the ornamentation of the tegmina, which in most Recent species is smooth. No veins could be seen in the forewing (tegmina), which is shorter than the abdomen, although there may have been a trace of a subcostal vein.

Suborder ARCHIDERMAPTERA

Diagnosis. Tegmina reaching well down abdomen. Tarsi 4–5 segmented.

Remarks. Only one family and genus, from the Upper Jurassic of Kazakhstan, are currently known in this suborder.

Family PROTODIPLATIDAE Martynov, 1925*b*

Diagnosis. As suborder.

The new genus described below is provisionally placed in this family. Western Europe, Jurassic.

Genus *BREVICULA* nov.

Type species. *Brevicula gradus* sp. nov. Lower Lias, U.K.

Diagnosis. Tegmina strongly punctate, reaching at least to second abdominal segment. Coxae short, rounded.

Name. 'A little thing'.

Brevicula gradus sp. nov.

Figs 3–4

DIAGNOSIS. As genus.

NAME. 'A step'.

DESCRIPTION. Head prognathous; antennae incomplete, multisegmented. Possible Y-shaped suture on head. Thorax rounded. Tegmina strongly punctate, probably reaching third abdominal segment, rather slender (and possibly pointed but incomplete apically). Hindwings indistinct. Abdomen parallel-sided but terminal segment rounded. Terminal process possibly at least two-segmented, elongate. Legs cursorial, slender. Femora slightly thickened; 4–5 segmented tarsi.

HOLOTYPE. In.53993 (Fig. 3); Flatstones, Black Ven, Charmouth, Dorset. Jackson colln. Dimensions: Body 10 mm (including cerci); cerci 1·5–2 mm. Tegmina 4·4 mm.

PARATYPE. In.51036 (Fig. 4); data as holotype.

DISCUSSION. The strongly punctate tegmina conceal most of the folded wings in the fossil. Consideration was given to the possibility that the specimens represented a nymphal orthopteran or a brachypterous adult orthopteran, but the lateral displacement of the tegmina, which appear to be devoid of veins, would be unusual in these, but would not be unexpected in a fossilized dermapteran. It is not possible to count the exact number of tarsal segments, of which there are certainly four and may well be five. The apical cerci are difficult to interpret. In one specimen there is an indication that they may be segmented, perhaps with two segments, but in the other there is a longitudinal separation into two rather slender, and apparently lightly sclerotized, processes (forceps). The only coxa showing is on the foreleg where it is clearly short and rounded; this condition is regarded as more primitive than the long conical coxae of the Blattopteroidea. However, Hennig (1981) took the opposite view and said that the short coxae of the Dermaptera could have been a derived character.

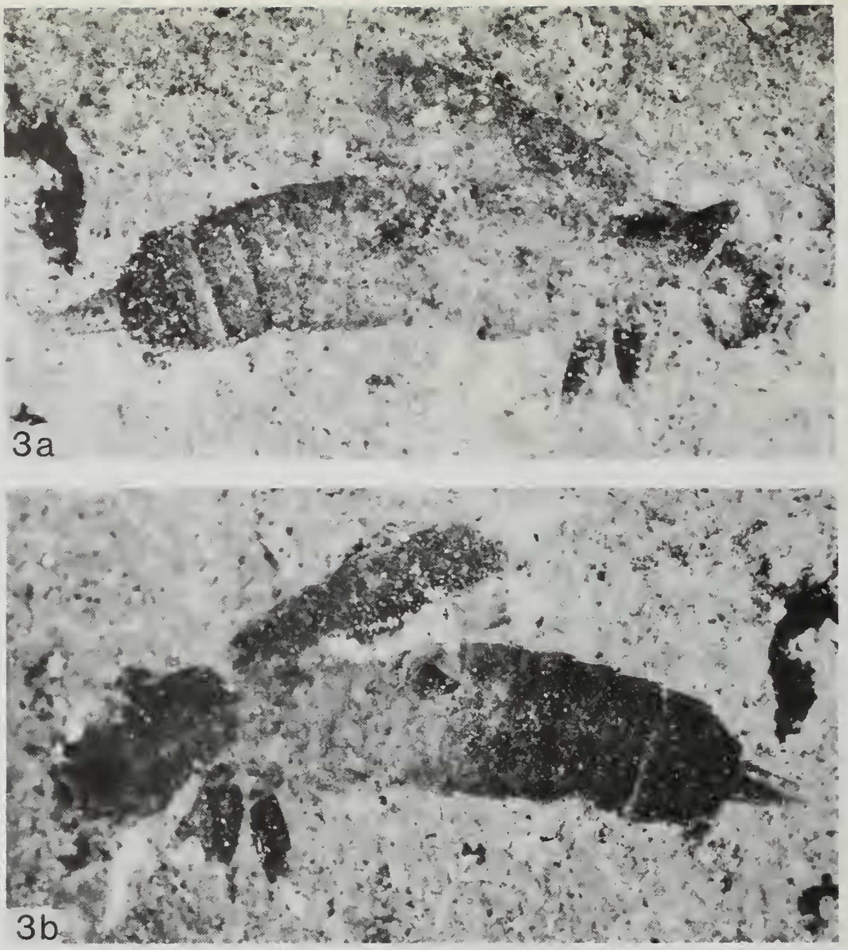
Order **ODONATA**, dragonflies

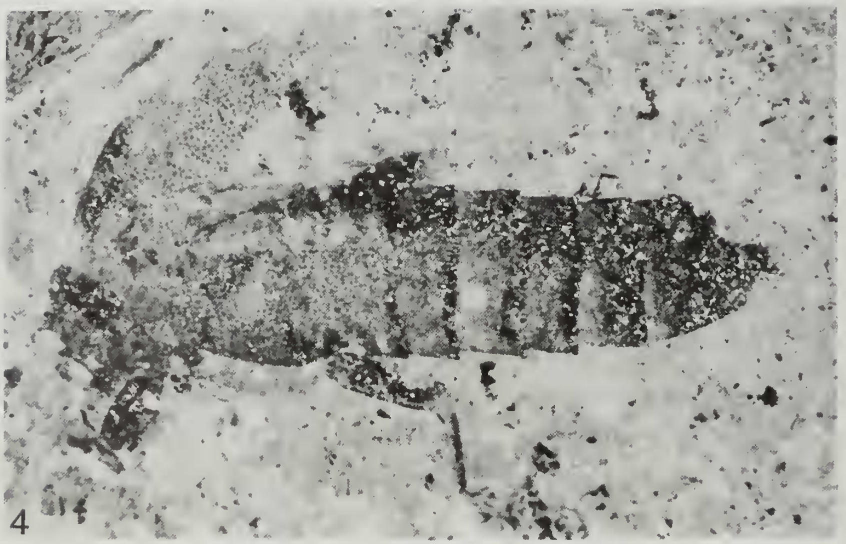
There is still some dispute over the major classification of this order. Much of our information is based on the work of Tillyard & Fraser (1938–40) and of Fraser (1957) although Carle (1982) reviews some aspects of their phylogeny. A recent interpretation of the classification within the order by Pritykina (1980) differs considerably from the earlier work. The traditional classification (Tillyard & Fraser 1938–40, Cowley 1942, Fraser 1957 and most textbooks) uses three main suborders in the Odonata, the Anisoptera, Zygoptera and Anisozygoptera, although Fraser (1957) listed four more suborders for fossil species (Protozygoptera, Archizygoptera, Meganisoptera and Protoanisoptera). The Anisoptera and Zygoptera are widely used in the literature although the latter is sometimes regarded as paraphyletic (Hennig 1981). It is, however, within the Anisozygoptera that there has been most controversy. An outline definition of the three suborders used here and based on Fraser (1957) is given below.

In the Anisoptera, in both fore and hind wings, a cross-vein divides the discoidal cell into an anterior and a posterior triangle. Both these triangles may be further subdivided by cross-veins.

The Zygoptera have the same shaped fore and hind wings, generally with a narrow base to the wing. The wings have either an open or a closed discoidal cell below the arculus. In some genera (e.g. *Hemiphlebia* Selys) the discoidal cell may be open in the forewing and closed in the hindwing; more frequently both wings have a closed discoidal cell. Within the Zygoptera further subdivisions are made based on the shape of the discoidal cell and the number of antenodal veins.

The Anisozygoptera of Handlirsch are known mostly as fossils from the Mesozoic and there are only two living species of *Epiophlebia* Calvert that are placed in this suborder; this is the





Figs 3–4 *Brevicula gradus* gen. et sp. nov. (Dermaptera). Fig. 3, **holotype**, In.53993. a, part, 10 mm long. b, counterpart. Fig. 4, paratype, In.51036.

traditional concept. But Imms (1970: 307) stated 'it is not easy to frame a definition of this suborder (i.e. Anisozygoptera) to embrace its many Mesozoic forms'. In the Recent species the base of the wing is narrow while it is broad in the fossils. The discoidal cell is normally square in the hindwing but may be a different shape in the forewing. Asahina (1954) divided the Anisozygoptera into two superfamilies, placing the two living species of *Epiophlebia* in the Superfamily Epiophleboidea, separating them from the fossil species which he placed in the Heterophleboidea. He stated that the Epiophleboidea are 'most closely related to the Heterophleboidea of the Lias period' and then added 'if considered from venational characters there seems to be enough reason to include both groups within the same suborder' (i.e. Anisozygoptera).

Pritykina (1980) emphasized, however, the differences between the fossil and Recent 'Anisozygoptera' in her classificatory diagram (1980: fig. 611). She also used a different nomenclature for the various groups; her names are given in brackets in the following account. Her diagram can be interpreted as showing a sister-group relationship between the Anisoptera (Libellulomorpha) and Recent Anisozygoptera (Epiophleboidea). She had an enlarged group called Lestomorpha in which she placed the Zygoptera and all the Mesozoic 'Anisozygoptera'. She clearly regarded the Mesozoic anisozygopteran genera as being more closely related to the Zygoptera than to the Anisoptera or Recent Anisozygoptera.

Zygoptera first appear in the fossil Record in the Permian (*Permagrion* Tillyard). There is still some dispute over the earliest Anisopteran but there is no doubt they were much later than the Zygoptera. *Liassogomphus* Cowley from the Upper Lias in Gloucestershire was accepted as a true anisopteran by Tillyard (1925) and Cowley (1942), although Fraser (1957) places it in the Anisozygoptera. There is a typical anisopteran triangle in *Liassogomphus* and Pritykina (1968) described several Jurassic Anisoptera. Hennig (1981) placed *Liassogomphus* as possibly the stem-group of the Anisoptera and Anisozygoptera. In the present study the Mesozoic fossils are placed provisionally in the Anisozygoptera pending a further analysis of the major classification of the Odonata.

If the fossil and Recent Anisozygoptera (as traditionally interpreted) form a monophyletic group, it is obvious that it was far more abundant in the Mesozoic than it now is, having only two living species. Comparing all the present-day Odonata with their fossil record and considering the species diversity, one may conclude that Odonata were possibly more abundant in the Mesozoic than at the present day; it is interesting to speculate on factors which might have allowed this. The most obvious one is the almost complete lack of birds as predators in the early Mesozoic. No doubt insects, including dragonflies, were the prey of some of the Mesozoic pterosaurs, but it was the appearance of insect-eating birds later in the geological record that provided the first real competition for the predatory aerial dragonflies. Probably it was competition for the aerial insects as food as much as direct predation on the dragonflies themselves which materially affected their abundance. Thus while dragonfly-like forms had been the only or the main aerial predators of flying insects since the Upper Carboniferous, their zenith was passed in the Mesozoic and the present-day species are the remnants of a much larger Mesozoic fauna. Even the size has decreased, from the giant dragonfly-like predators of the Palaeozoic with wingspans of 600 mm, to the present-day forms, the largest of which is well under 200 mm. Many of the Mesozoic species had a larger wingspan than any of the living species. While the birds may have been one of the factors in the faunal decline of the Odonata, there were probably others that have not yet been identified.

Suborder **ANISOZYGOPTERA**

Family **LIASSOPHLEBIIDAE** Tillyard, 1925

Diagnosis. Fore- and hindwings differ in venation. Discoidal cell often open posteriorly in forewing. Usually only two antenodal cross-veins.

Western Europe, Jurassic.

Genus *LIASSOPHLEBIA* Tillyard, 1925

Type species. *L. magnifica* Tillyard 1925: 13, by original designation.

Diagnosis. Only two antenodals. Discoidal cell irregular, not square or rectangular.

Jurassic, Europe.

Liassophlebia pseudomagnifica sp. nov.

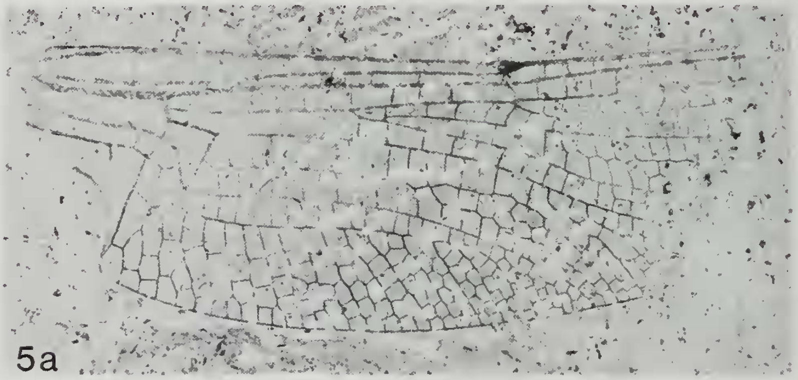
Fig. 5a, b

1962 *Liassophlebia magnifica* Tillyard; Zeuner: 162; pl. 27, fig. 1.

Diagnosis. *Liassophlebia* with double row of polygonal cells in area between M and Cu.

Name. Not true *magnifica*.

Description. Single hindwing; apical half missing. Venation as in Fig. 5a. Costal vein thick at base; two antenodals, 7 mm apart. Arculus strongly recurved. Discoidal cell closed. Node approximately 25 mm from wing base.



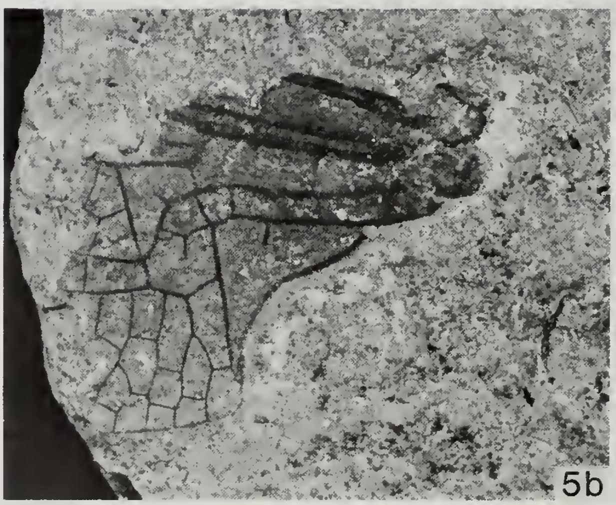


Fig. 5 *Liassophlebia pseudomagnifica* sp. nov. (Odonata). **Holotype**, In.64000. a, part, hindwing, 39 mm long. b, counterpart, wing base.

HOLOTYPE. In.64000; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: length (incomplete) 39 mm, estimated wing length 50–52 mm.

DISCUSSION. The holotype has been prepared by degagement, i.e. uncovering more of the fossil by removal of overlying rock. This has revealed more details than were available to Zeuner (1962), who identified this specimen as *L. magnifica* Tillyard. Comparison of the newly-revealed basal part of the wing with the type of *L. magnifica* shows that, apart from some differences in cell shapes, *L. pseudomagnifica* is also substantially smaller. In *L. magnifica* the node, at 35·4 mm from the base, is almost equidistant from the tip of the wing. In the incomplete wing of *L. pseudomagnifica*, on the other hand, the node is 25 mm from the base of the wing: if the two wings had similar proportions, this would mean a total wing length of 50 mm for *L. pseudomagnifica*. The wingspan of *L. magnifica* was about 140 mm, whereas that of *L. pseudomagnifica* was only 100 mm.

The possibility that *L. pseudomagnifica* was the (smaller) male of *L. magnifica* was considered. Variation in wing length in the Recent Anisozygoptera was discussed by Asahina (1954), who showed that a maximum variation within one species was 4 mm in the male and 3 mm in the female, well below the difference between *L. magnifica* and *pseudomagnifica*; they are clearly not individual variants of one species. The number of cells in the cubital and anal areas, the shape of the discoidal cell and the reduction in number of antenodals separate *L. pseudomagnifica* from Recent species of *Epiophlebia*, while the fossil species, *L. jacksoni*, is much smaller.

Specimen In.49213 was also incorrectly identified as *L. magnifica* by Zeuner (1962: 162); it may well be *pseudomagnifica* but no further development has been possible.

Liassophlebia jacksoni Zeuner, 1962
Fig. 6

1962 *Liassophlebia jacksoni* Zeuner: 162; pl. 25, figs 1, 2.

Only a small amount of development of the specimen has been possible since Zeuner examined it and this does not materially alter his interpretation of the species. A further 8 mm of wing has been exposed, giving a preserved length of 75 mm. Zeuner's estimate of wing length of 83 mm is reasonable.

HOLOTYPE. In.53999; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln.

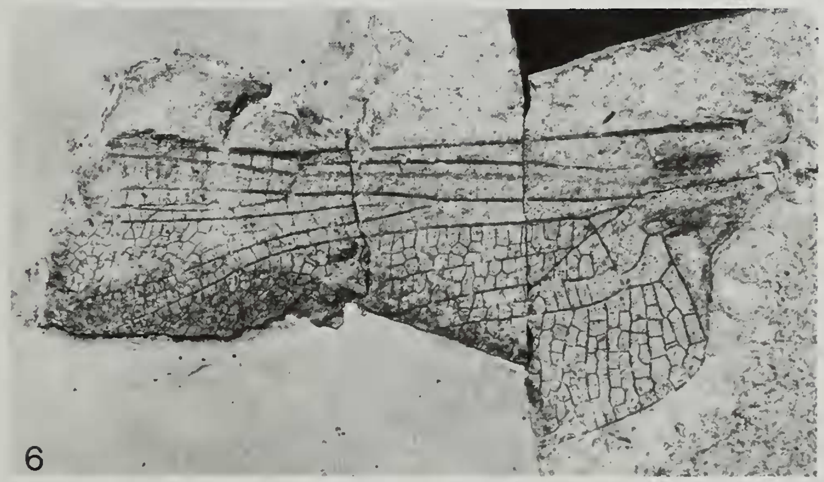


Fig. 6 *Liassophlebia jacksoni* Zeuner (Odonata). Holotype, In.53999. Hindwing, 75 mm long.

Liassophlebia gigantea Zeuner, 1962
Fig. 7a, b

1962 *Liassophlebia gigantea* Zeuner: 163; pl. 27, fig. 2.

This forewing has been developed further since it was examined by Zeuner but the newly-revealed parts do not alter his interpretation. The full shape of the discoidal cell is revealed as elongate and lying almost at right angles to the main axis. The discoidal cell is closed at the posterior margin, unlike *L. magnifica* where the cell is open in the forewing, although closed in the hindwing. The development of the wing has exposed the nodal area and also clearly shows the strongly curved base of the costa.

Holotype. In.51030; Woodstones, Black Ven, Charmouth, Dorset. Jackson colln.

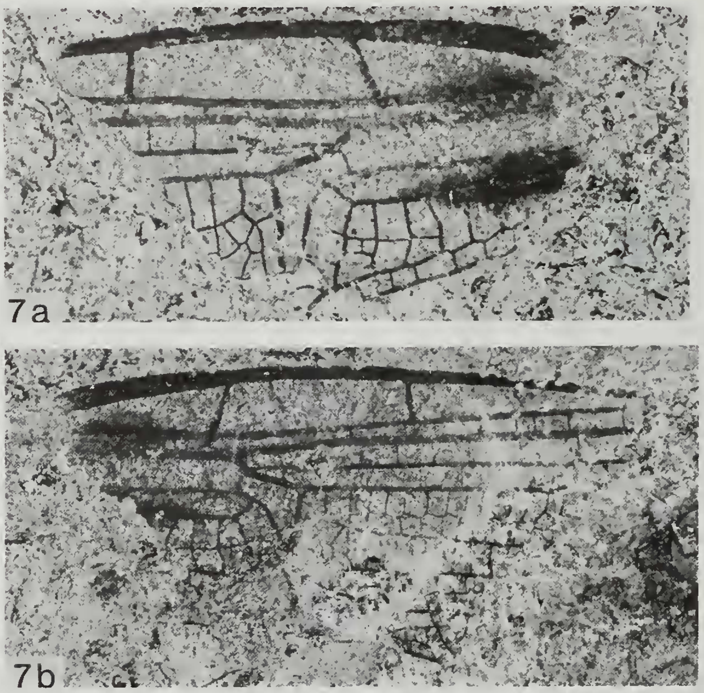


Fig. 7 *Liassophlebia gigantea* Zeuner (Odonata). Holotype, In.51030. a, part, wing length *c.* 33 mm (incomplete). b, counterpart, wing length *c.* 24 mm (incomplete).

Liassophlebia anglicanopsis (Zeuner) 1962, comb. nov.
Fig. 8a, b

1962 *Petrophlebia anglicanopsis* Zeuner: 160; pl. 24, figs 1, 2.

By degagement it has been possible to develop this specimen, revealing far more than could be seen when Zeuner examined it. The incomplete wing seen by Zeuner was only 34·5 × 15 mm, but using the fine pneumatic drill to remove the overlay, 64 × 20 mm of it has now been revealed. In spite of this, Zeuner's original estimate of the total wing length (80 mm) is still considered reasonable. He commented that 'the poor condition of the wing, with its corroded edge, suggests prolonged drifting' (Zeuner 1962: 161), but this is untenable in the light of the new evidence revealed by development. The wing was not in poor condition but the 'corroded' edges were buried immediately below an ammonite (*Asteroceras obtusum* J. Sowerby): when the

8a

8b

Fig. 8 *Liassophlebia anglicanopsis* (Zeuner) (Odonata). Holotype, In.49573. a, part, hindwing 64 mm long. The white patches near the anterior margin are the remains of an ammonite: this was overlying the wing and caused the slight deformation, visible as slightly wavy lines along the anterior margin. b, counterpart, ammonite not removed.

ammonite shell was removed the wing was found to have been deformed by its weight pressing on it while the Jurassic mud was wet, but the wing had not been torn. The wavy shape of the wing reflects the shape of the ammonite pressed into it. It appears the wing had stuck on the mud and the ammonite had come to rest on it, deforming it slightly. The alternative hypothesis, that the wing had washed up against a partly buried ammonite shell, does not seem tenable from a study of the specimens. There was no sediment between the wing and the ammonite shell, suggesting that their burial was simultaneous.

The further development of the wing has revealed most of the basal area, together with the discoidal cell; this has shown that the generic position assigned by Zeuner was incorrect. No further development of the second specimen (In.59376) mentioned by Zeuner has been possible and it may or may not be conspecific with *L. anglicanopsis*.

Holotype. In.49573; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln.

Genus *HYPSOTHEMIS* Pritykina, 1968

Type species. *Hypsothemis jurassica* Pritykina 1968: 41, by original designation.

Diagnosis. Both distal angles of quadrangle (discoidal cell) acute. Posterior margin (of cell) slightly longer than anterior side. Posterior margin of wing without strong anal angle. Anal vein turns towards margin of wing level with centre of quadrangle (Pritykina 1968, in part).

Jurassic, Asia.

Hypsothemis fraseri sp. nov.

Fig. 9

1962 *Liassophlebia magnifica* Tillyard; Zeuner: 162 (part).

DIAGNOSIS. Discoidal cell with broader apical side. Single row of veins form large cells in between M and Cu.

NAME. After the late F. C. Fraser, a specialist on Odonata.

DESCRIPTION. Incomplete hindwing with two antenodals. Discoidal cell with very long distal side and row of slightly sinuous veins between M and Cu. Large cell below discoidal between CuA and CuP at angle to long axis of wing; the cell may be divided but this is not clear in the specimen. Anal cells in regular arrangement along basal margin. Some anterior basal sclerites preserved with long fine hairs attached.

HOLOTYPE. In.59106; Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: 40 × 16 mm (incomplete). Distance between antenodals, 5·5 mm.

OTHER MATERIAL. In.59109; data as holotype.

DISCUSSION. Degagement of this wing has allowed a study to be made of many more veins than were available to Zeuner (1962), who incorrectly identified it as *L. magnifica* Tillyard. In particular all the cells in the basal area of the wing have been exposed. The holotype is broadly similar to *Hypsothemis jurassica* Pritykina, but differs in having three rows of cells in the anal and four in the postcubital areas, whereas *H. jurassica* has only two in the anal and three in the postcubital area and is a smaller species. The genus *Hypsothemis* was previously known only from the type species from Asia. The Dorset specimen has part of the hairy base of the wing preserved near the costal margin. The exact shape of the cell (quadrangular) immediately below the discoidal cell is not entirely clear in the fossil but is probably longer than wide.

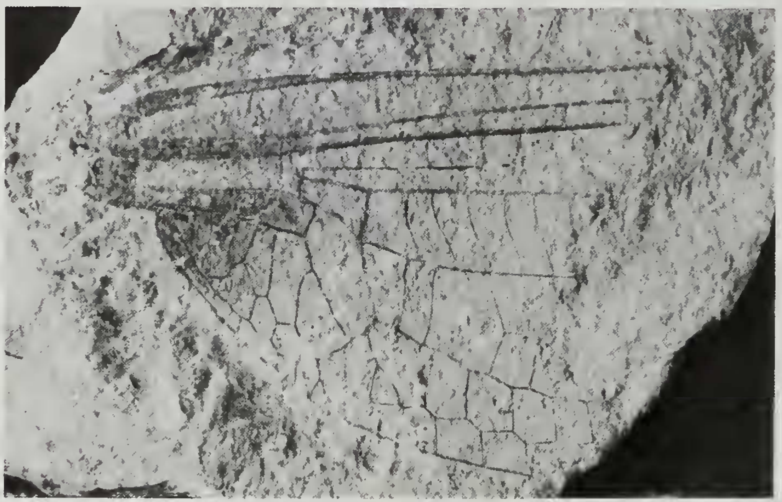


Fig. 9 *Hypsothemis fraseri* sp. nov. (Odonata). **Holotype**, In.59106, hindwing, 40 mm long.

Family **ARCHITHEMISTIDAE** Handlirsch, emend. Cowley, 1942

Genus ***DORSETTIA*** nov.

TYPE SPECIES. *Dorsettia laeta* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Discoidal cell elongate, almost rectangular. Cross-veins between M and Cu, CuA and CuP almost parallel, forming row of elongate cells between each pair of veins.

NAME. From the county of Dorset.

The genus is very distinct from other Mesozoic genera and its relationship is not clear. Provisionally it is placed near *Diastatommites* Handlirsch, but differs in the large single cells in the area between the cubital veins.

Dorsettia laeta sp. nov.

Fig. 10a, b

1962 ? *Diastatommites liassina* (Strickland); Zeuner: 164; pl. 27, fig. 3.

DIAGNOSIS. As genus.

NAME. 'Joyful'.

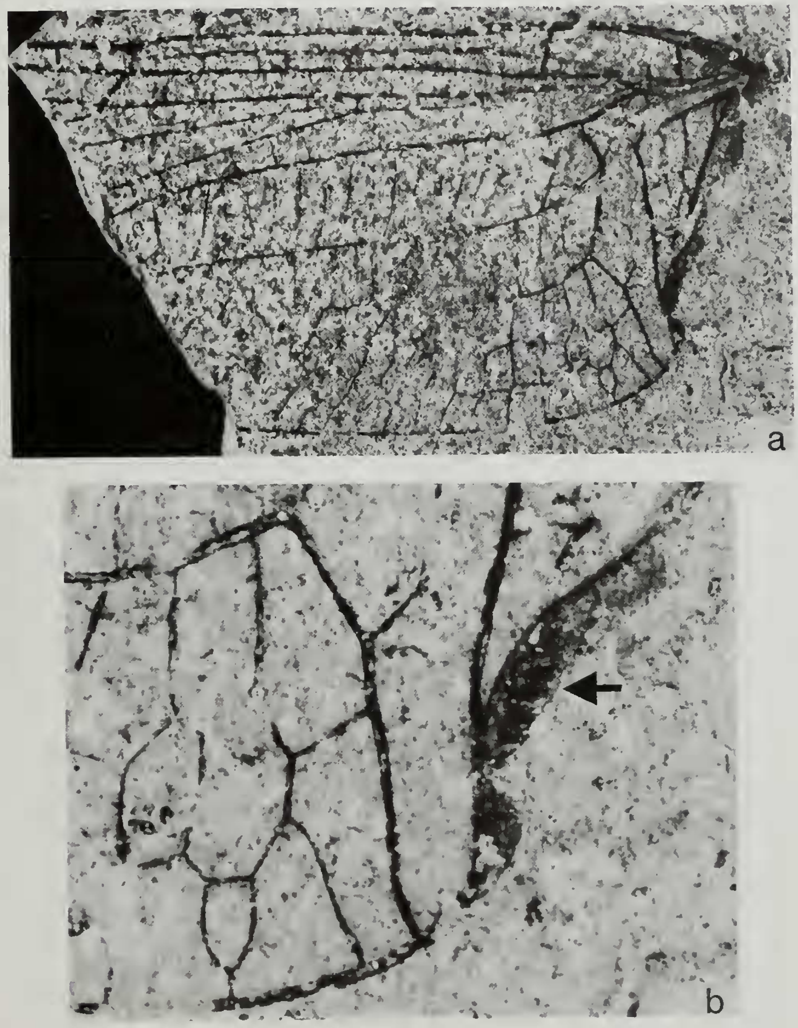


Fig. 10 *Dorsettia laeta* gen. et sp. nov. (Odonata). **Holotype**, In.59375. a, hindwing, 37 mm long. b, base of same wing to show hairs (arrowed).

DESCRIPTION. Incomplete male hindwing. Probably only two antenodals. Node 30 mm from base of wing. Setal bases along veins in discoidal and cubital rows. Sub-discoidal cell elongate. Anal cells elongate, almost at right angles to long axis of wing. Basal hind margin sclerotized and hairy.

HOLOTYPE. In.59375; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 37 mm (incomplete) × 13·5 mm. Estimated total wing length 60–65 mm.

DISCUSSION. Very little of this specimen was seen by Zeuner, who provisionally identified it as a species of *Diastatommites* (Zeuner 1962: 164). Degagement has cleared all the overlying rock. The wing node, 30 mm from the base of a wing 13–14 mm wide, suggests a very broad, though relatively short, wing. The discoidal cell of *Dorsettia* is similar in shape to many Mesozoic Anisozygoptera.

The specialization of the basal part of the wing is similar to many Recent Corduliinae (Anisoptera): this type of broad, modified base is found in males where sexual dimorphism in wing shape occurs. Hence the specimen of *Dorsettia* is considered to be a male; in this species there was probably sexual dimorphism, in which case the female wing would show simpler structure. Perhaps we have here the earliest example of such sexual dimorphism in the Odonata.

Family **HETEROPHLEBIIDAE** Handlirsch, 1906

Genus ***HETEROPHLEBIA*** Westwood, 1849

TYPE SPECIES. *Agrion buckmanni* Brodie 1845, by monotypy (Westwood 1849: 32). Upper Lias, U.K.

The single incomplete specimen from Dorset lacks the costal margin and much of the anterior part of the wing. There is also a fault in the rock in the area of the triangle. The cubital veins curve backwards strongly but the preservation is such that this specimen is only provisionally placed in *Heterophlebia*.

MATERIAL. In.49246; Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Length 15 mm, estimated wing length 30–40 mm. Distance between antenodals, 5·5 mm.

Odonata indet.

In.53895 and In.53972, mentioned by Zeuner (1962: 164), are possibly parts of *Liassophlebia* wings.

Order **ORTHOPTERA**, grasshoppers and crickets

The Dorset Lower Lias is very rich in orthopterous fossils, which make up 14% of the insect species. The fauna includes some of the largest Jurassic insects, like *Protohagla langi* Zeuner which had a wingspan of nearly 150 mm. Some of the fossils are almost complete specimens while others are represented by wings or legs only. There are also a number of isolated, unassociated insect legs, many of which are clearly orthopterous, and several of the saltatorial types were found (Figs 30–32). But it has not been possible to associate these isolated legs with particular species, although some were found not far removed from bodies of orthopterous insects. This implies that the legs, which in the Orthoptera are easily broken off the dead insect, can only have been separated from one another at a short distance from the final deposition site, particularly as a few specimens still have the legs attached. The area from which the Dorset fossils were derived was clearly rich in highly diversified Orthoptera.

The classification used in the following section is based on Sharov, 1968 (English translation, 1971).

Suborder **ENSIFERA**

Superfamily **OEDISCHIIDEA**

Fossils of the nine families in the Oedischiidea of Sharov have been found from the Upper Carboniferous to the Lower Cretaceous (Sharov 1968). The forewings are long and rather narrow in proportion to the length and lack any stridulatory organs.

Family **ELCANIDAE** Handlirsch, 1906

Genus ***ARCHELCANA*** Sharov, 1968

Type species. *Elcana britannica* Handlirsch, by original designation of Sharov (1968: 35).

Diagnosis. Elcanids with Sc simple; C with short branches and a three-branched cubital vein. More anal veins than species of *Elcana* (Sharov 1968).

Lower Lias, western Europe.

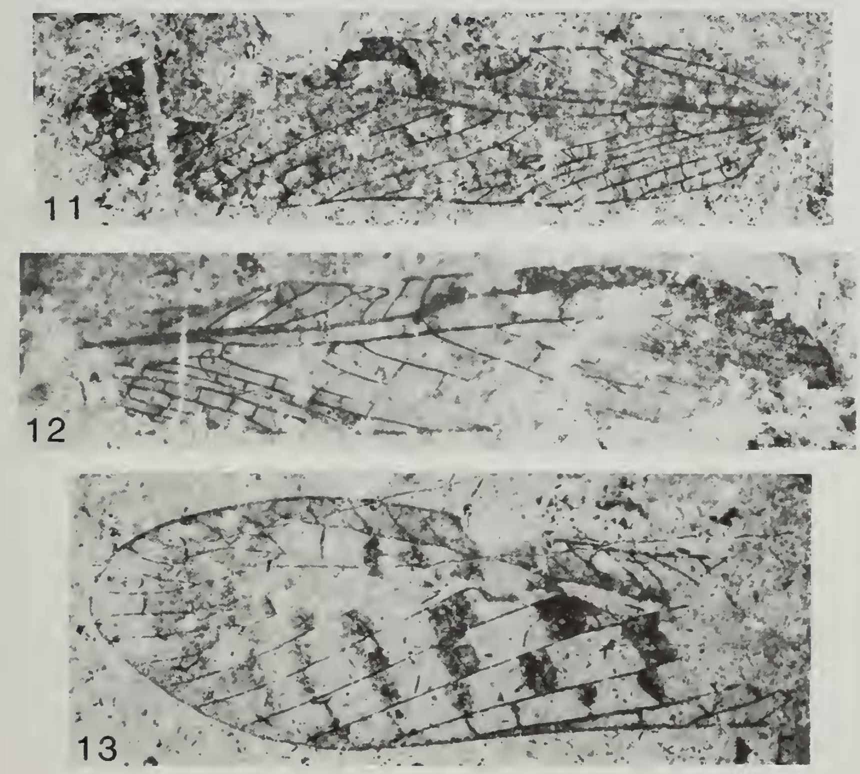
Archelcana durnovaria sp. nov.

Figs 11–15

Diagnosis. As genus, but with prominent cross-vein from M–Cu near base.

Name. Latin name of Dorchester.

Description. Forewing, costal vein short with lateral veinlets; subcostal unbranched. R_1 arises before division of MA and MP. Rs long, running forward with anterior branches to margin.



Figs 11–13 *Archelcana durnovaria* sp. nov. (Orthoptera). Fig. 11, **holotype**, In.59162, forewing, 20 mm long. Fig. 12, paratype, In.59377, forewing. Fig. 13, paratype, In.53922, forewing.

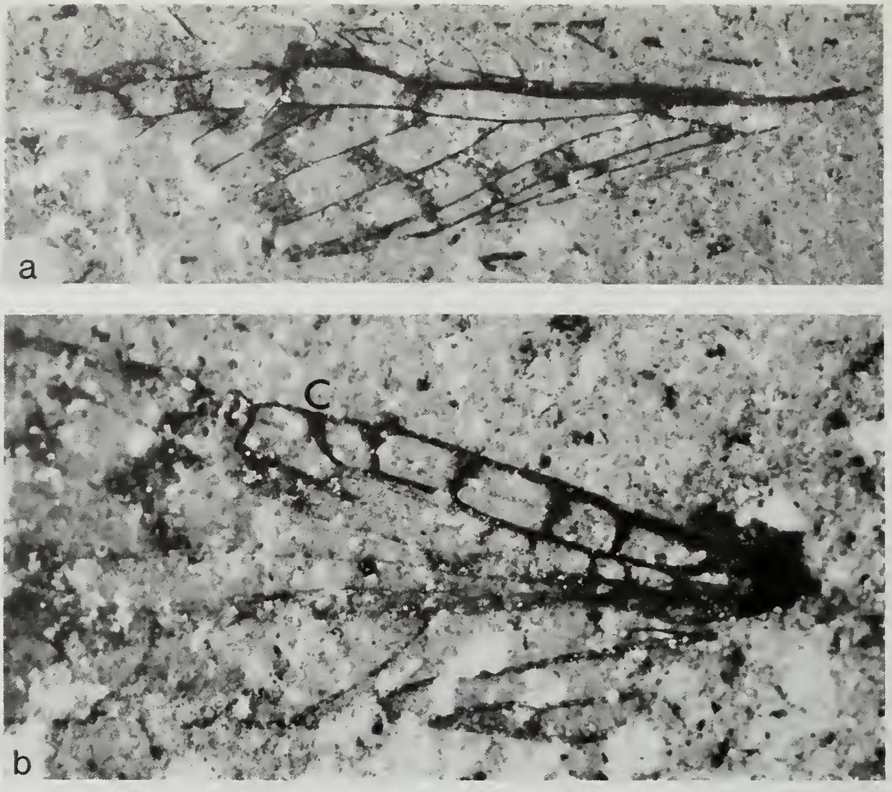


Fig. 14 *Archelcana durnovaria* sp. nov. (Orthoptera). Paratype, In.59381, forewing. a, part. b, counterpart. C = cells in anal area of wing (see p. 129).

Medial vein curves from broad stem of R + M and divides into MA and MP. Several parallel branches arise from MA. Prominent cross-vein from M to Cu where CuA curves forward. Posterior cross-vein from junction with CuA_2 to R + M. CuP straight with CuA_1 and CuA_2 curved forward off it. Three anal veins with cross-veins. Long (9·2 mm), curved ovipositor; segmented antennae (incomplete); eyes and antennal base preserved.

HOLOTYPE. In.59162 (Fig. 11); Woodstone, Black Ven, Charmouth, Dorset; Jackson colln. Dimensions: Wing length 20·1 mm, width 4·4 mm.

PARATYPES. In.51029, In.53894, In.53922 (Fig. 13), In.59377 (Fig. 12), In.59381 (Fig. 14), In.64005, In.64038.

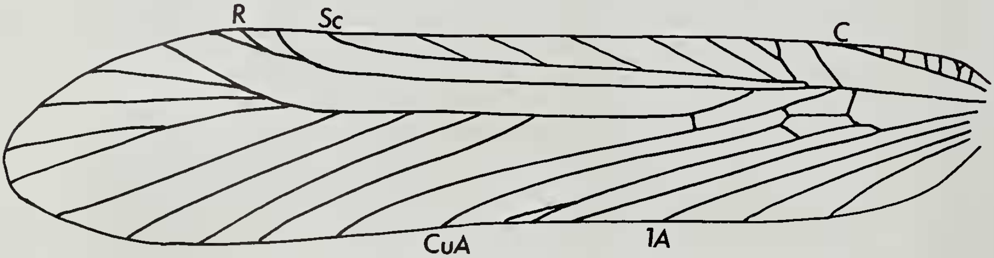


Fig. 15 *Archelcana durnovaria* sp. nov. (Orthoptera). Diagram of wing venation. 1A = first anal vein, C = costal vein, CuA = cubital veins, R = radial veins, Sc = subcostal vein.

OTHER MATERIAL. In.49203, In.49580, In.49600, In.49614, In.53900, In.53906, In.53956, In.53976, In.59139, In.59151, In.59358A, In.64001, In.64006, In.64028.

DISCUSSION. The genus *Elcana* can be separated from *Archelcana* by the number of cubital veins, two in the former, three in the latter. The type of *Elcana*, *E. tessellata* Westwood from the Purbeck beds, has only two cubital veins and has a few branches toward the anterior margin from Sc; these are absent in *Archelcana*.

Including the new species, there are three species of *Archelcana*. *A. shurabica* Sharov, from the Lower Jurassic of Asia, has additional branches on the end of the first anal vein and the subcostal vein reaches further towards the apex than in *A. durnovaria*. *A. britannica* (Handlirsch) is from the Lower Lias of Warwickshire and most closely resembles the new species: it can be distinguished by the relatively long cross-vein Mu–Cu and the shape of the base of CuA_1 and CuA_2.

Sharov (1968) considered that there was a precostal vein in this genus. This can be seen in Fig. 14b at the bottom right as an inverted Y-shaped vein. This specimen shows strongly sclerotized anal cross-veins (Fig. 14b, 'C'). This suggests that there may well have been a more heavily sclerotized forewing, probably similar to many Recent Orthoptera. The veins on the part and counterpart have separated unequally, making the two halves look rather different.

A special feature of *Archelcana* is the development of three cubital veins although the anterior one could be considered as CuA + MP. The antennal segments preserved in one specimen (In.64028) indicate that there was a long filiform antenna. The ovipositor preserved on the same specimen is slightly curved, finely pointed and evidently strongly sclerotized. Traces of the rest of the body of In.64028 are indistinct but one of the anal cerci is preserved.

Although probably all the specimens included amongst 'Other Material' are *A. durnovaria* some of the diagnostic characters are indistinct and these specimens are therefore excluded from the series of paratypes.

Family **TRIASSOMANTIDAE** Tillyard, 1922

This family was originally associated with the Mantidae by Tillyard (1922). Sharov (1968) redefined it on the basis of the short and narrow precostal area and the anterior median vein forking level with, or apically to, the origin of the radial sector vein. At present this family is known from the Triassic of Australia and Siberia.

Genus ***ORICHALCUM*** nov.

TYPE SPECIES. *Orichalcum ornatum* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Triassomantids with slender wings and an anastamosis between Rs and MA; branched costal vein which reaches the anterior margin slightly anterior of level of fork of CuA and CuP.

NAME. 'Brass'.

Orichalcum ornatum sp. nov.

Figs 16, 21

DIAGNOSIS. As genus.

NAME. 'Equipped'.

DESCRIPTION. Costal vein with short side-branches; subcostal vein extends well along front margin of wing towards apex, running closely parallel with R for much of its length. Rs branches well anterior to apex of costal vein, slightly anterior to fork of CuA and CuP. Rs short, joins MA which then has four more branches to wing margin. Three or four post-medial branches. Cu relatively simple, broadly forking well before middle of wing with forked CuA and simple CuP. Anal area long, ending just in front of origin of Rs. Anal veins close together. Strongly reticulated cells over apical portion of wing, cross-veins numerous in basal part. Some strongly pigmented areas visible, probably representing original pattern.

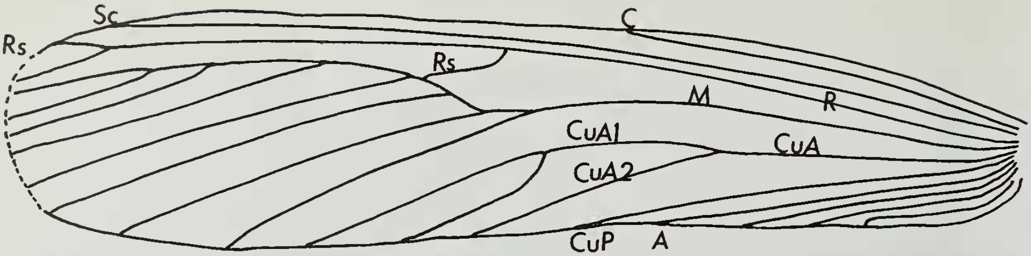


Fig. 16 *Orichalcum ornatum* gen. et sp. nov. (Orthoptera). Diagram of forewing venation. C = costal vein, CuA = anterior cubital, CuP = postcubital, M = median vein, R = radial veins, Sc = subcostal vein.

HOLOTYPE. In.53983; Birchi nodule, Black Ven, Charmouth, Dorset. Jackson colln. Dimensions: 26 mm (slightly incomplete) × 5 mm. Wing length estimated 28 mm.

DISCUSSION. Sharov (1968) considered *Ferganopterus* Sharov, from the Lower Lias of Asia, as the most primitive of the family. *O. ornatum* broadly resembles this species and (whether considered primitive or not) both have a highly specialized venation. *Orichalcum* can be distinguished from *Ferganopterus* by having three or four anal veins and a longer branched costal vein. The fusion of the radial sector with the anterior median vein occurs in many of the fossil Oedischiidea. Amongst the Dorset Lias Orthoptera, *Orichalcum* is unique in having a slender wing and relatively simple cubital venation. Some of the patterning has been preserved on the wing and the type of preservation indicates that the forewing was probably strongly sclerotized.

O. ornatum was amongst the last of the specialized triassomantids which arose in the early Trias and extended into the Jurassic. It is one of the few insects to be found in the Birchi nodules from the Turneri Zone of the Dorset Lias, and by one ammonite subzone (perhaps 300,000 years) is older than the insects from the Obtusum Zone, from which the majority of Dorset Lias insects were collected.

Superfamily **GRYLLIDEA**

Family **HAGLIDAE** Sharov, 1968

Sharov (1968) separated the Haglidae from the Gryllidae by the position of the posterior medial and anterior cubital veins. In the Haglidae the post-medial and anterior cubital are displaced to the posterior margin of the wing, whereas in the Gryllidae they are in the middle of the wing, almost parallel to the wing margin. In the gryllids, apart from the characters mentioned, the presence on the forewings of the mirror and associated sound-producing organs and the characteristic sharp curvature of the forewing, which produces the box-like cover of the hindwings and body, are distinctive. These synapomorphic characters indicate that the Gryllidae are a reasonably homogeneous and monophyletic group. The species that remain in the Superfamily Gryllidea, when the Gryllidae *s. str.* are removed, are broadly covered by Sharov's Haglidae; this is almost certainly a polyphyletic group, containing both true close relatives of *Hagla* and also probably stem-group gryllids. However, for the purpose of this faunal study, the species which do not fall into the Gryllidae *s. str.* are placed in the Haglidae, with the proviso of the polyphyletic nature of this group.

Genus ***HAGLA*** Giebel, 1856

Hagla cf. ***gracilis*** Giebel

cf. 1856 *Hagla gracilis* Giebel: 264.

In.59167 is an incomplete specimen which is similar to *H. gracilis* Giebel from the Lower Lias of Gloucestershire. The subcostal vein and radial sector are close together and there are strong cross-veins in the cubital and anal areas; these cross-veins are often curved. The wing is folded and no exact comparison has been possible with the described species of *Hagla.*

Genus ***REGIATA*** nov.

TYPE SPECIES. *Regiata scutra* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Grylloids with strongly pitted forewings. M and Cu parallel near the base. MA curving sharply forward. Subcostal veinlets sinuous.

NAME. 'Bordered'.

Regiata scutra sp. nov.

Figs 17–20

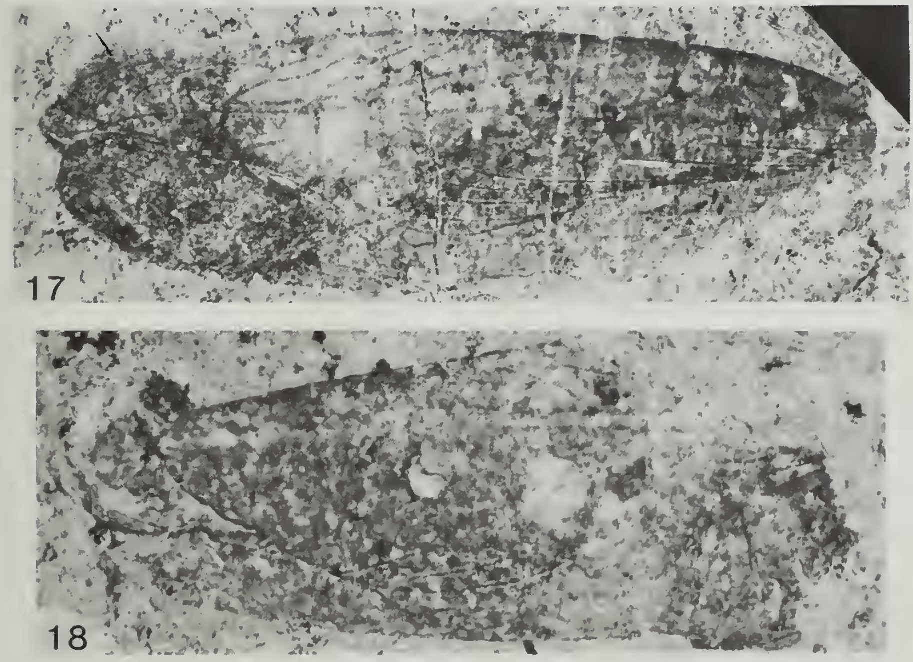
DIAGNOSIS. As genus.

NAME. 'A salver'.

DESCRIPTION. Forewing with short costal vein near base in broad costal/subcostal area. Subcostal vein reaching well beyond middle of wing, subcostal area broad in basal half; subcostal veinlets strongly marked with pits. R almost parallel to Sc for much of its length. M curving strongly towards hind margin before dividing into MA and MP. MA curves forward, MP curves backwards parallel with Cu to wing margin. Anterior branches from MP arise almost at right angles to it. Apical part of median and cubital veins clearly parallel and slightly curved (easily distorted in fossilization). Apex of wing narrower. Anal area very strongly punctate, reticulations clear. Size range: 16·7–21·5 × 6·3 mm.

HOLOTYPE. In.64027 (Fig. 17); Flatstones, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 21·4 × 6·3 mm.

PARATYPES. In.49568, In.49597, In.59146 (Fig. 19), In.59169 (Fig. 20), In.64007 (Fig. 18), In.64037.



Figs 17–18 *Regiata scutra* sp. nov. (Orthoptera). Fig. 17, **holotype,** In.64027, forewing, 21 mm long. Fig. 18, paratype, In.64007, forewing.

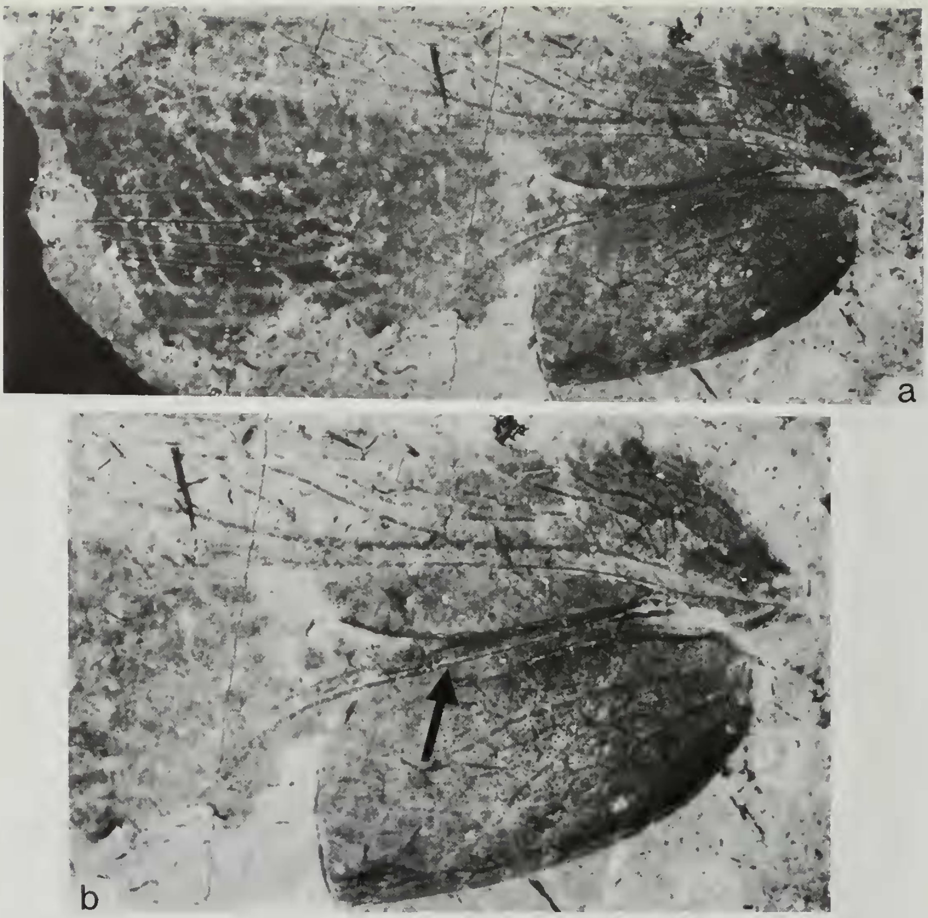


Fig. 19 *Regiata scutra* sp. nov. (Orthoptera). Paratype, In.59146, forewing. b, enlargement of anal area and wing base. Note break in wing in front of anal area (arrowed) caused when the curved wing was flattened. Wing membrane heavily spotted.

OTHER MATERIAL. In.59392.

DISCUSSION. This species is similar to the grylloid *Karataogryllus gryllotalpiformis* Sharov, from the Jurassic of Asia, but differs in the shape of the median vein and the very sinuous subcostal vein. *R. scutra* was probably similar to Recent gryllids where the wings are folded over the back. When these were flattened during fossilization they split at the base of the wing, seen in Fig. 19b (arrow) as a fine break between the anal area and the rest of the wing. *R. scutra* also had the apex of the wings rolled together or even curled up as shown by In.64007 (Fig. 18). When the surface of the rock is wet the fossil appears to be covered in granules which, when examined dry, are seen to be tiny pits. Although these pits are denser in the anal area they occur over most of the forewing. The pitting shows up clearly in the subcostal area where they are arranged regularly along the subcostal veins. The anterior median and postcubital veins on some specimens are thickened; these thickened veins were almost certainly slightly raised above the wing and may have formed part of the stridulatory mechanism, but there is no sign of the mirror which, in Recent forms, is bounded by CuP and a branch of CuA. Vein 1A, which is also part of the stridulatory mechanism in Recent species, is, however, prominent in the fossil. *R. scutra* can be distinguished from *Hagla gracilis* Giebel, which is common in some Lower Lias

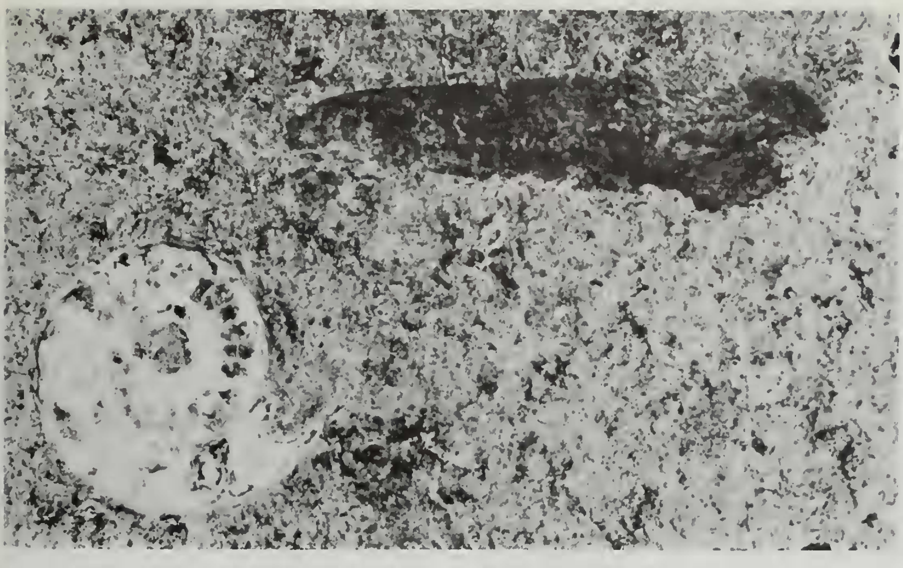


Fig. 20 *Regiata scutra* sp. nov. (Orthoptera). Paratype, In.59169, wing, 27 mm long. This is on the same bedding plane as an ammonite.

deposits in Britain, by a number of characters. The displacement of the postmedian and anterior cubital veins towards the posterior margin occurs in both *Hagla* and *Regiata* but they differ considerably in the form of the subcostal veins and the arrangement of the anal veins. *R. scutra* has a less complex, though equally broad, costal area similar to *H. gracilis*, but the median and cubital veins are nearly parallel towards the apex, suggesting a rolled or curved apex to the wing. The split apparent in most of the fossils between the anal area plus Cu + M and the rest of the wing is consistent with the flattening of the wing in life, which could have been held in the typical gryllid-like (box-like) fashion over the body. Until further studies are made of the Haglidae *s. lat.* the classification of *Regiata* as a haglid must remain provisional (see p. 130).

Genus ***PROTOHAGLA*** Zeuner, 1962

TYPE SPECIES. *Protohagla langi* Zeuner, by original designation. Lower Lias, U.K.

Protohagla langi Zeuner, 1962
Fig. 22

1962 *Protohagla langi* Zeuner: 165; pl. 26, figs 1, 2.

No new material of this species has been found since Zeuner originally described it. *P. langi* is a large insect and had a wingspan of about 150 mm. Zeuner (1962: 166) said that in this specimen (In.59018) the fore and hind wings had been nipped off simultaneously at their bases. He speculated that this had happened when the insect was caught, with the wings closed, by a predator over the land. However, examination shows that the underlying wing is another forewing, so Zeuner's hypothesis is untenable.

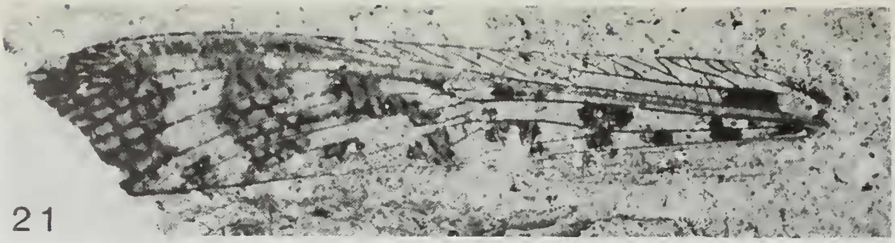
Family **GRYLLIDAE** Latreille, 1802

Genus ***PROTOGRYLLUS*** Handlirsch, 1906

TYPE SPECIES. *Protogryllus dobbertinensis* (Geinitz 1880), by subsequent designation of Zeuner (1939: 188). Lias, Europe.

DIAGNOSIS. Gryllids with distinct harp in male forewing but without mirror (Handlirsch 1906: 424).

21



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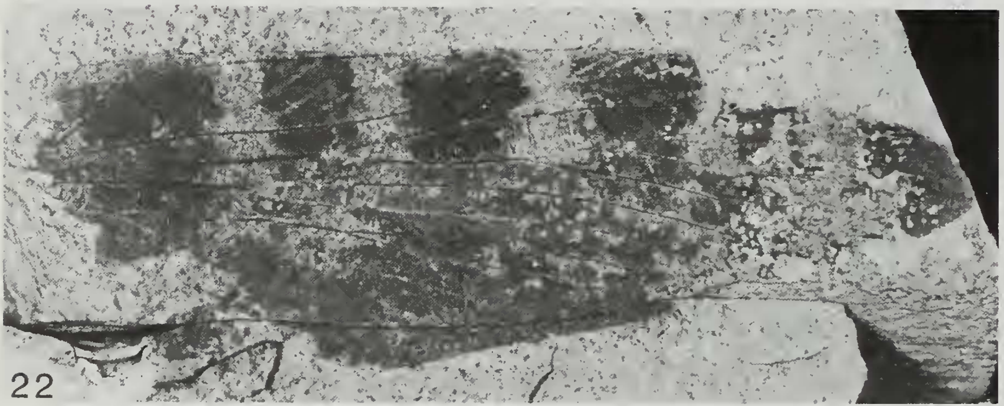
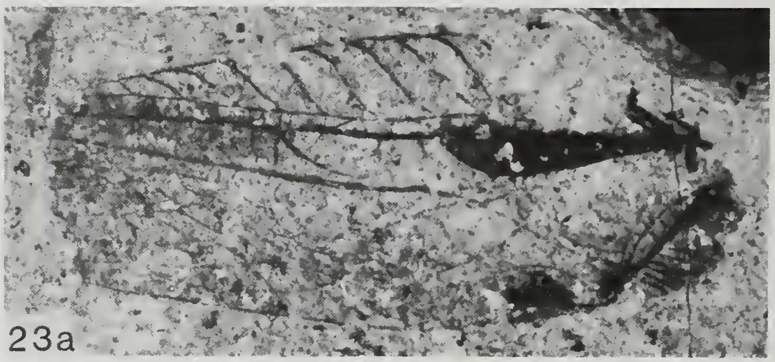


23a



23b

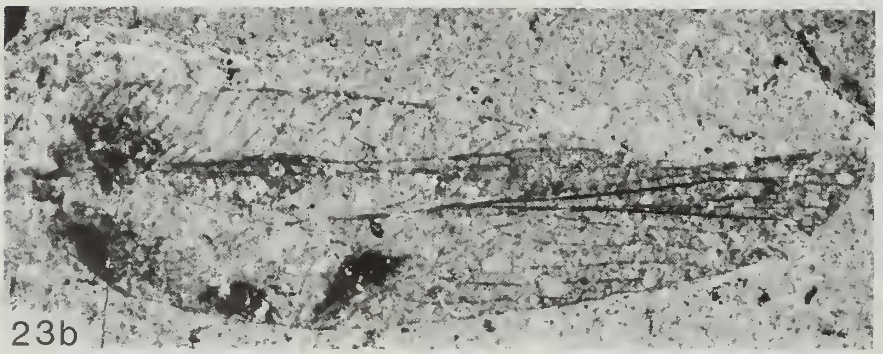


Fig. 21 *Orichalcum ornatum* gen. et sp. nov. (Orthoptera). **Holotype,** In.53983, forewing, 26 mm long. Note the patterning on the wing.

Fig. 22 *Protohagla langi* Zeuner (Orthoptera). Holotype, In.59018, forewing, 61 mm long.

Fig. 23 *Protogryllus magnus* Zeuner (Orthoptera). In.51016, forewing, 26 mm long. a, part. b, counterpart.

Protogryllus magnus Zeuner, 1937
Fig. 23a, b

1937 *Protogryllus magnus* Zeuner: 155.
1939 *Protogryllus* (*Archaegryllodes*) *magnus* Zeuner; Zeuner: 192.

Zeuner based the description of *P. magnus* on two incomplete male specimens, the holotype from the Upper Lias of Dumbleton, Gloucestershire and a second specimen from the Lower Lias of Binton, Worcestershire. Only slight differences have been found between these and the Dorset specimens. The curvature of the median vein, where it curves forward towards the radial, is more gentle in the Dorset specimens than in the holotype. Otherwise the size and rest of the venation are similar. Zeuner's figure of 22 mm wing length is based on the holotype and is probably an underestimate; even so, the Dorset specimens are larger and with the difference in localities, may represent a distinct species.

Zeuner (1937) placed *P. magnus* in the subgenus *Archaegryllodes* Haughton (1924) on the basis of the median and radial veins touching in the forewing. He likened it to a Triassic species, *A. stormbergensis* Haughton from South Africa. In 1939 Zeuner suggested that *Protogryllus grandis* Zeuner might be the female of *P. magnus*, but no further evidence for this hypothesis has been elicited from the Dorset specimens. There is more of the very specialized venation preserved in the Dorset specimens than in the holotype of *P. magnus*; the stridulatory area of the male forewing can be seen in Fig. 23a.

MATERIAL. In.44003, In.51016 (Fig. 23), In.51022, In.59373. Dimensions: 26·7 × 7·4 mm.

Genus ***MICROMACULA*** nov.

TYPE SPECIES. *Micromacula gracilis* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Gryllids with narrow wings, dense maculations. Anal area more extensive than subcostal area. Distinct fan present between Cu and M in centre of wing.

NAME. 'Small spot'.

Micromacula gracilis sp. nov.
Figs 24–25

DIAGNOSIS. As genus.

NAME. 'Slender'.

DESCRIPTION. Forewing with broad base, narrowing apically. Subcostal area reticulate; subcostal vein reaching costal margin well before middle of wing. Costal margin with distinct hump on basal part. Radial vein running roughly parallel to median vein along wing. Cu sharply angled along edge of anal area with CuP close and three anal veins. Whole wing covered with fine spots. Cubital with fan-shaped arrangement of branches to medial veins. Anal area larger than subcostal area, strongly reticulate and covered with spots.

HOLOTYPE. In.49230 (Fig. 24); Birchi nodule, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 11 × 2·6 mm, forewing; 12–13 mm, hindwing.

PARATYPES. In.49594, In.51041, In.53913, In.53934, In.53969, In.59126 (Fig. 25).

OTHER MATERIAL. In.53926, In.53973, In.64031.

DISCUSSION. The holotype of *M. gracilis* is from the Turneri Zone whereas most of the paratypes are from the younger Obtusum Zone. This is the only species certainly known to occur in both the Turneri Zone and Obtusum Zone, but for most species zonal age data is unavailable (see p. 110).

Specimen In.59126 (Fig. 25) has both forewings and part of the hindwings preserved. The hindwing is longer than the forewing and is membranous, but is heavily folded and no details of the venation can be seen. The forewings are strongly sclerotized and similar to those of many

Figs 24–25 *Micromacula gracilis* sp. nov. (Orthoptera). Fig. 24, **holotype,** In.49230. Fig. 25, paratype, In.59126, pair of forewings, length 11 mm.

Recent species. The wing was evidently curved round the body in life, as in modern gryllids, because the flattened fossil shows cracks in the position of original folds. *M. gracilis* was probably similar in appearance to the Recent species *Amsurgus lateralis* Chopard (Gryllidae, Trigonidiinae), a cricket from the Pacific area. The forewings of the Recent species are broadly patterned giving a reticulate appearance, and the surface is covered with small spots; these are larger on the veins, and from them hairs arise. Little is known of the biology of the Recent species, which is considered to be typically tree-dwelling, rather than ground-living.

Suborder **CAELIFERA**

Superfamily **LOCUSTOPSIDEA**

Family **LOCUSTOPSIDAE** Handlirsch, 1906

Genus ***LOCUSTOPSIS*** Handlirsch, 1906

TYPE SPECIES. *Locustopsis elegans* Handlirsch, by subsequent designation of Cockerell, 1915. (Handlirsch 1906: 421; Zeuner 1942: 8; Sharov 1971: 90–97). Trias–Upper Lias, Europe.

Diagnosis. CuA divides into three branches. Sc extends almost to apex of wing. R and M run separately to base of wing. M with three, rarely two, branches.

Locustopsis spectabilis Zeuner, 1942
Figs 26–28

1942 *Locustopsis spectabilis* Zeuner: 8; fig. 1.

Type locality. Strensham, Worcestershire; Upper Trias.

Discussion. This species was described by Zeuner on the basis of a single, slightly folded, forewing from Strensham and he mentioned a possible second specimen from Warwickshire. There are a number of specimens from Dorset which I attribute to this species, although they differ slightly from the holotype in the relative proportions of the wing; this could be due to the slight folding in the holotype. The Dorset specimens show a weakly-developed precostal vein while the actual costal vein is well developed with lateral branches. The subcostal vein reaches the wing tip while the radial, subcostal, median and cubital veins are separated almost to the base of the wing. The median vein divides into three branches; in some specimens the third branch comes off the postmedial while in others it comes off the antemedial. Most of the specimens from Dorset, and the holotype from Worcestershire, have a three-branched cubital vein, but two Dorset specimens (In.49591, In.51043 (Fig. 28)) have an extra branch, making a four-branched cubital. Recent Orthoptera have considerable intraspecific variation in wing venation (Ragge 1955) but, in Recent species, a four-branched cubital is unusual. The rest of the venation of these two specimens is similar to the other Dorset specimens and they are considered to be merely intraspecific variants.

Material examined. In.49203, In.49208, In.49565 (Fig. 26), In.49586, In.49591, In.49593 (Fig. 27), In.49600, In.49614, In.50992, In.51001, In.51035, In.51043 (Fig. 28), (? In.53900), In.53908, In.53914, In.53917, (? In.53984), In.59121, In.59131, In.59357, In.59358A, In.59367, In.64039.

Dimensions. 22–29 mm.

Order **PHASMATODEA**, stick-insects

Superfamily **XIPHOPTERIDEA**

Family **AEROPHASMATIDAE** Martynov, 1928

This family was based originally on specimens from the Jurassic of Karatau. Sharov (1968) commented on traces of dense short hairs on these specimens, which are also clearly visible on the new species from Dorset.

Genus ***DURNOVARIA*** nov.

Type species. *Durnovaria parallela* sp. nov. Lower Lias, U.K.

Diagnosis. Elongate wing with roughly parallel veins. Costal vein simple, unbranched; costal area densely hairy. Median three-branched with MP and Cu having a common stem.

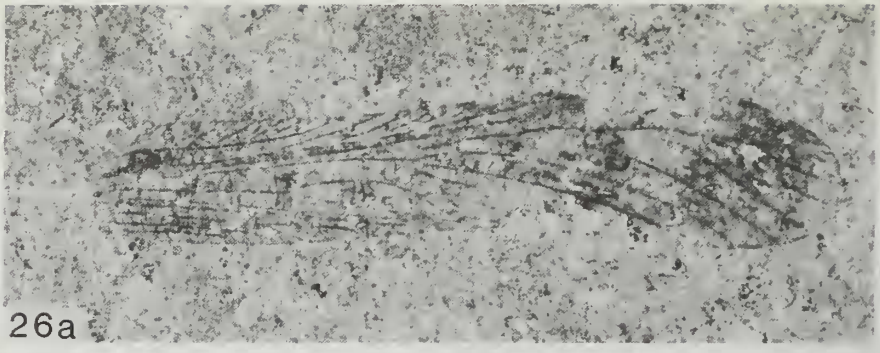
Name. Latin name of Dorchester.

Durnovaria parallela sp. nov.
Figs 29, 33–34

Diagnosis. As genus.

Name. 'Parallel'.

Description. Precostal, costal and much of subcostal areas very hairy, rest of wing strongly pigmented and probably hairy. Sc short, reaching to costal margin approximately level with first fork of radial vein. Four radial veins (plus radial sector) almost parallel along wing. Median and radial veins clearly fused at base of wing. Median (strictly M + CuA) divides very early into MA, which again forms three branches, and MP/Cu branch. The latter divides into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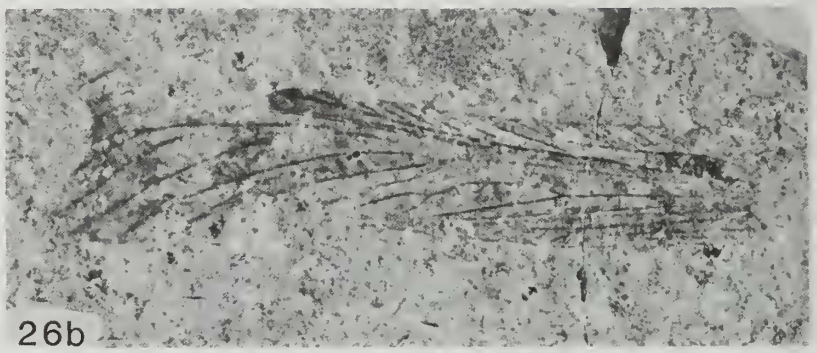
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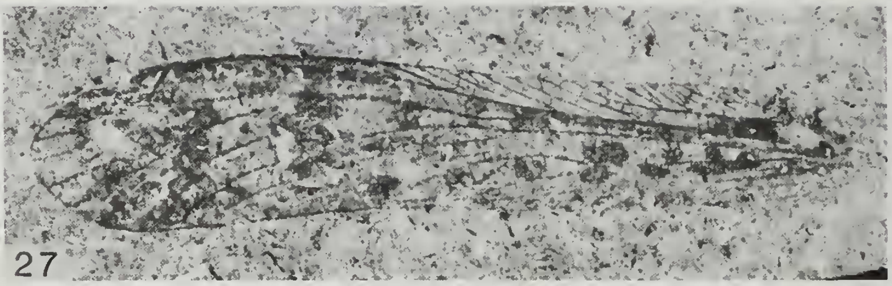
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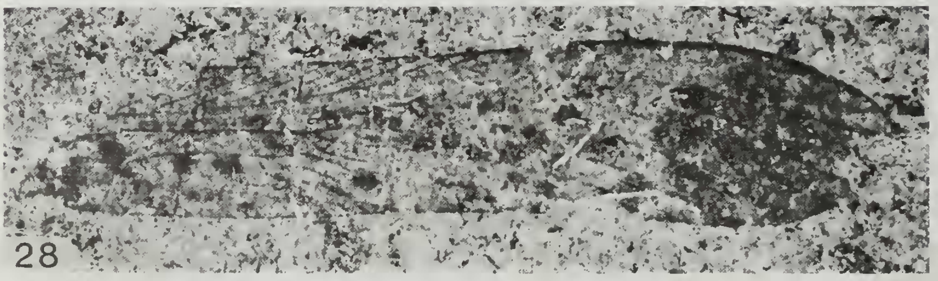
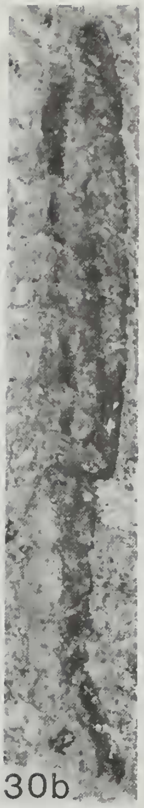

28

Figs 26–28 *Locustopsis spectabilis* Zeuner (Orthoptera). Fig. 26, In.49565, forewing, 24 mm long. a, part. b, counterpart. Fig. 27, In.49593, forewing. Fig. 28, In.51043, forewing.



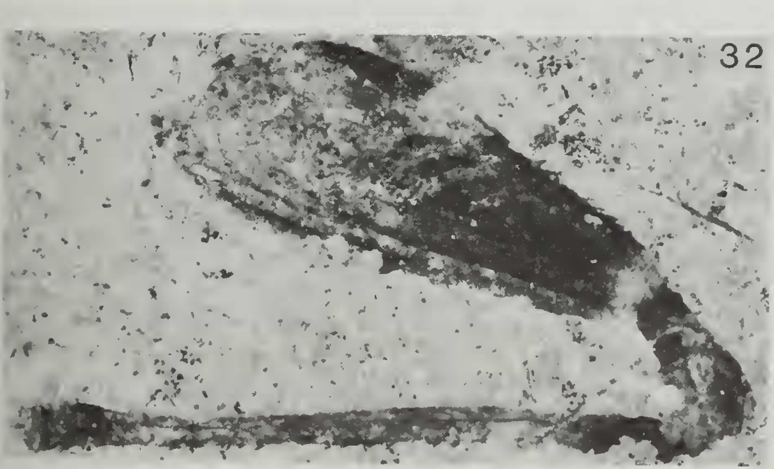


Fig. 29 *Durnovaria parallela* gen. et sp. nov. (Orthoptera). **Holotype,** In.59171, counterpart. See Fig. 33.

Figs 30–32 Orthoptera, saltatoria-type legs. Fig. 30, In.59127, tibia and tarsi, total length 24 mm. Stout spines on tibia. a, part. b, counterpart. Fig. 31, In.59391, femur 10·9 mm, tibia 10 mm. Note ridge of spines along both. Fig. 32, In.53919, femur 9·2 mm.

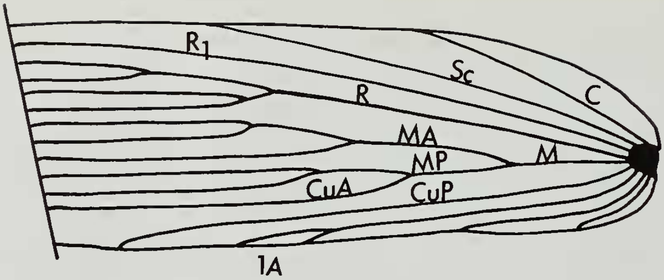


Fig. 33 *Durnovaria parallela* gen. et sp. nov. (Orthoptera). Diagram of forewing venation. A = anal area, C = costal vein, Cu = cubital veins, M = median veins, R = radial veins, Sc = subcostal vein.

two, a postmedial and anterior cubital. The posterior branch of M + Cu forms CuA. CuP comes off near the base of M from the common stem of M + CuA and runs unbranched to the wing margin. The first anal has a short apical branch, the second is nearly as long but unbranched, while the third is short. There are many small reticulations in the area between 2A and the wing margin.

HOLOTYPE. In.59171 (Figs 29, 34); Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 34 × 7·7 mm; estimated wing length 36 mm.

DISCUSSION. This species is separated from the Chresmodidae (*sensu* Sharov, 1968) by the branching of the postmedian and anterior median veins. It differs from *Aerophasma* Martynov in having a weakly-developed cubital vein and in the division of the anterior median vein into two branches. The long parallel-vein appearance is typical of the Xiphopteroidea. The very hairy nature of the wing, particularly clear in the anterior basal part of the wing, is characteristic of the Aerophasmatidae, a family currently known from the Jurassic of the U.S.S.R. The other families in the Xiphopteroidea are Triassic (Xiphopteridae, Aeroplanidae), Jurassic (Necrophasmatidae) or Cretaceous (Cretophasmatidae). All are regarded as related to, though not necessarily direct ancestors of, modern stick-insects (Phasmidae).

Fig. 34 *Durnovaria parallela* gen. et sp. nov. (Orthoptera). **Holotype,** In.59171, part, forewing, 34 mm long. See Fig. 29.

Order **HEMIPTERA**, plant bugs

Suborder **HOMOPTERA**

Six homopterous insects occur in the Jackson collection. Three of these are considered to belong to a species in the Cicadidea, one is unidentifiable but in the same superfamily, one is placed in the Cicadellidea and the last is in the Superfamily Fulgoridea. Currently there are six species of Mesozoic Homoptera known from the U.K.; these are three species of *Margaroptilon* (Handlirsch 1906) and one of *Homopterites* (Handlirsch 1906); both genera are in the Cicadellidae, one in Tettigarctidae and one in Cicadidae (Whalley 1983).

Superfamily **CICADIDEA**

Family **TETTIGARCTIDAE** Bekker-Migdisova, 1949

There are only two living species of this family which is common in the fossil record from the Triassic onwards. Species of several genera are known from the Mesozoic while the sister-group, Cicadidae, are rare in the Mesozoic (Whalley 1983). The fossils from Dorset, which have similar venation to *Shuraboprosbole* Bekker-Migdisova, are very much smaller. The vein which represents the base of the median, linking it and the anterior cubital to the postcubital as a cross-vein, cannot be seen in the Dorset specimens and was probably not present.

Genus ***PARAPROSBOLE*** nov.

TYPE SPECIES. *Paraprosbole rotruda* sp. nov. Lower Lias, Dorset, U.K.

DIAGNOSIS. Base of M + CuA thickened and curved. Cross-vein from M + CuA missing.

NAME. Like *Prosbole*, but distinct.

Paraprosbole rotruda sp. nov.

Figs 35–36

DIAGNOSIS. As genus.

NAME. A genus of Recent moths (Heinrich 1956: 225).

DESCRIPTION. Base of M + CuA curved and thickened. R clearly divided as far as nodal line. CuA and anal veins unbranched. Nodal line double, pigmented.

HOLOTYPE. In.59374 (Fig. 35); Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: Base of wing to nodal line 12–13 mm. Nodal line, from anterior to posterior wing margins, 8–9 mm. Total wing length 20–22 mm.

PARATYPES. In.48162 (Fig. 36), In.64395.

DISCUSSION. None of the wings is complete but comparison of the base of the wing (holotype) and the width of the wing at the nodal line with all the specimens suggests they are all conspecific, even though one is represented only by the apical part of the wing. They differ from the Triassic *Cicadoprosbole* in having fewer short branches on the radial vein near the apex of the wing. In specimen In.48162 (Fig. 36) the ambient vein is clear, with traces of the membrane distal to this visible.

Tettigarctidae, gen. et sp. indet.

The single specimen is incomplete and cannot be identified further than to family. It has a clearly preserved nodal line and parts of a few apical veins can be seen. There are some strongly marked sclerotized areas towards the centre of the front margin of the wing but the whole wing is much smaller than in *Paraprosbole*.

MATERIAL. In.51011 (not figured). Dimensions: Apical vein *c.* 4·5–5 mm. Nodal line *c.* 4·5 mm. Basal part of wing to nodal line *c.* 7·5 mm.

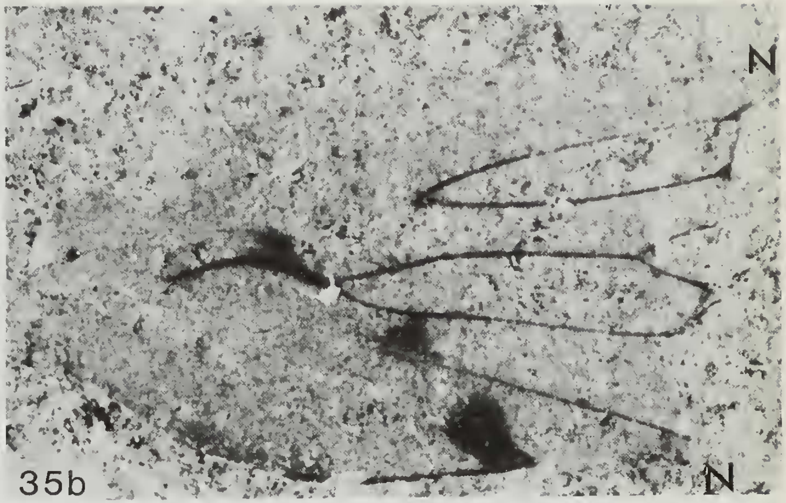
Superfamily **CICADELLIDEA**, gen. et sp. indet.

Fig. 37

The single specimen does not have the nodal line as clearly preserved as in the Tettigarctidae but has a strongly curved R + M + Cu. Some of the apical veins are preserved.

MATERIAL. In.49225. Dimension: Wing length *c.* 8 mm.


35a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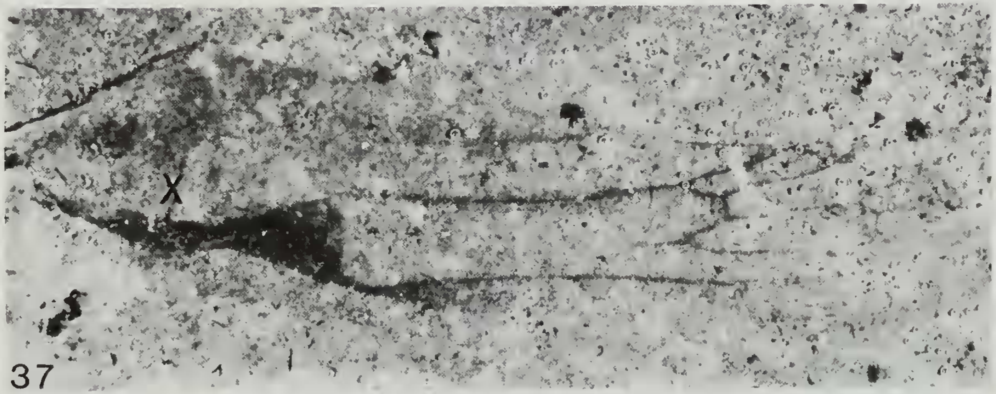
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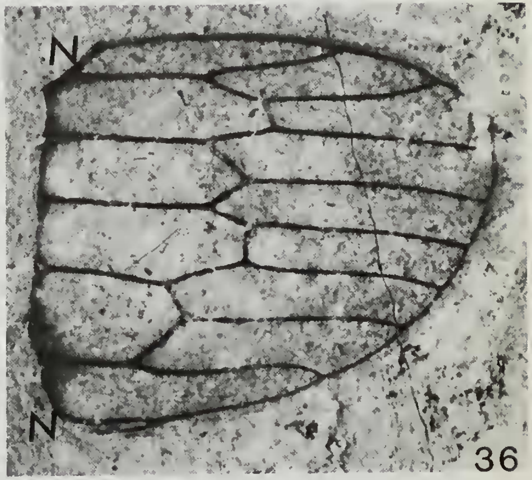
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Figs 35–36 *Paraprosbole rotruda* gen. et sp. nov. (Homoptera). Fig. 35, **holotype,** In.59374. N-N marks position of nodal line, which is about 8 mm long. a, part. b, counterpart. Fig. 36, paratype, In.48162. N-N = nodal line, approx. 8 mm long.

Fig. 37 Cicadellidea, gen. et sp. indet. (Homoptera). In.49225. X = base of radial + medial + cubital veins. Wing approx. 8 mm long.

Superfamily **FULGORIDEA**

Family **CIXIIDAE** Spinola, 1839

Genus ***MESOCIXIELLA*** Martynov, 1937

TYPE SPECIES. *Mesocixiella asiatica* Martynov, by original designation. Upper Triassic and Lower Jurassic, U.S.S.R.

Mesocixiella (?) ***fennahi*** sp. nov.

Fig. 38

DIAGNOSIS. Fulgoroid with short branches to R_2. Front margin of tegmina straight.

NAME. After Dr R. G. Fennah, specialist in Fulgoroids.

DESCRIPTION. Head regularly curved, narrow. Rostrum reaching to metathorax. Sc vein long, R probably unbranched near apex. Two wings overlap and some of the veins visible in the figure are from the lower wing. M forks with several more apical forks. Eyes just visible, trace of antenna below eye.

HOLOTYPE. In.53942; Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Head to tip of wing, 5·9 mm; Wing approx. 4 mm. Head to tip of abdomen, 3·7 mm.

DISCUSSION. I am grateful to Dr R. G. Fennah for comments on this specimen in which he indicated the general cixiid-like appearance, although pointing out that some of the diagnostic features cannot be seen. Cixiids are an extant group with a long fossil history from the Permian (Rohdendorf 1962). *M.* (?) *fennahi* is only provisionally placed in the genus *Mesocixiella*.

Suborder **HETEROPTERA**

The Heteroptera are currently the subject of a joint research project by the present author with W. R. Dolling and Y. I. Popov. The paper (in press) will contain a detailed taxonomic account of the new species and a discussion of their affinities. The basic information from this study will be summarized here for use in the evaluation of the fauna.

Thirty specimens of Heteroptera from the Dorset Lias occur in the Jackson collection, and one additional specimen from the same locality is preserved in the City of Bristol Museum and Art Gallery.

The results of the study showed that, while there were aquatic Heteroptera which could be placed in Recent families, all the terrestrial species belonged to extinct families. This confirms similar results with the Heteroptera from the Upper Lias of Germany found by Popov & Wootton (1977), where they were unable to place any of the terrestrial species in extant families. In the forthcoming revision of the Heteroptera of the Dorset Lias, one species is placed in Archegocimicidae, eight in the Pachymeridiidae, two in the Corixidae, and four (including the specimen from the Bristol Museum) in the Belostomatidae. Of the remaining 15 specimens, 14 are placed in the Infraorder Cimicomorpha and will be put in a new family, while the remaining specimen is in the Infraorder Leptopodomorpha and will also be placed in a new family. The proposed names for the various taxa which will appear in the joint paper are not given here to avoid nomenclatural complications, but the registration numbers will allow correlation between the general discussion here and the subsequent descriptions of these species in the joint paper.

Infraorder **CIMICOMORPHA**

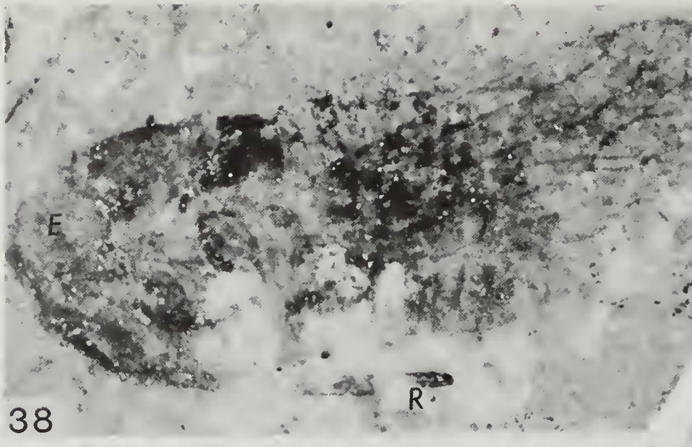
Family **ARCHEGOCIMICIDAE** Handlirsch, 1906

Archegocimicidae, gen. et sp. indet.

In.51007 is part of a wing which is provisionally referred to this family.

Family nov. 1

This family is erected to include the series of 14 specimens, all with clear cuneal and medial fractures and with the head, thorax and abdomen covered with short curved bristles.



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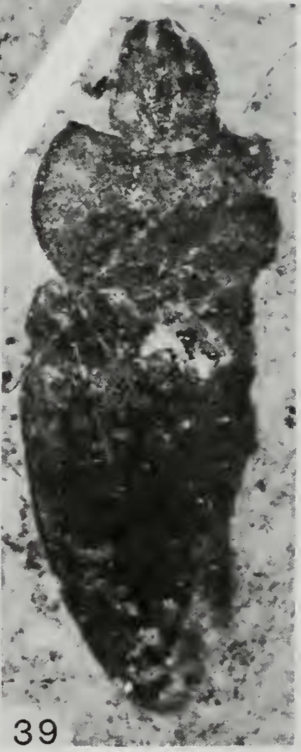

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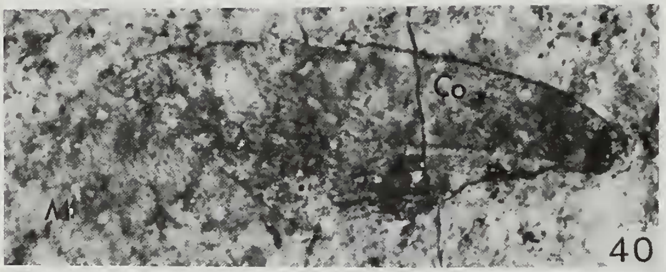

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Gen. et sp. nov. 1A

Figs 39–40

DIAGNOSIS. Head elongate, slightly longer than pronotum. Eyes small, hairy. Legs slender, rather short with femora scarcely reaching beyond body margin. Cuneal and medial fracture present. Pronotum strongly transverse, its lateral margins explanate and embracing the head.

MATERIAL. Four specimens from Black Ven, nine specimens from Stonebarrow, one specimen from Charmouth. In.49216, In.49243, In.49567, In.49576, In.49589, In.51048, In.53909, In.53986, In.53995, In.59104, In.59128 (Fig. 40), In.59137 (Fig. 39), In.59147, In.59358B. Dimensions: 8·8–10 mm body length. Jackson colln.

DISCUSSION. This is a very distinctive species of Heteroptera with a characteristically shaped head and prothorax, and conspicuous curved setae. Judged on the number of specimens in relation to the total number of Heteroptera in the collection, this species was common in the area from which the Dorset Lias insects were derived.

Infraorder LEPTOPODOMORPHA

Family nov. 2

This family is erected for a single species and genus from the Dorset Lias.

Gen. et sp. nov. 2A

Fig. 41

DIAGNOSIS. Pronotum with narrow anterior collar and transverse sulcus dividing it into smaller anterior and larger posterior lobes. Forewing with cuneal and medial fracture; membrane clearly differentiated from corium. Forewings greatly widened in costal area. Pronotum, scutellum, clavus and corium finely punctate.

MATERIAL. Black Ven, In.59152. Dimensions: 5·4 × 3·5 mm wing. Jackson colln.

DISCUSSION. Although the head is missing from the single specimen, the rest of the body is sufficiently well preserved to show characters of the new family.

Infraorder PENTATOMOMORPHA

Family PACHYMERIDIIDAE Handlirsch, 1906

A family with a number of species and genera described from the Mesozoic.

Gen. et sp. nov. 3A

DIAGNOSIS. Forewing narrow, as in *Pachymeridium* Geinitz, but with three branches of the radial vein arising close together near the apex of the medial fracture. Clavus and corium punctate, with cross-markings in 'herring-bone' pattern.

MATERIAL. Four specimens from Black Ven, three specimens from Stonebarrow. In.49566, In.51039, In.53901, In.53941, In.59105, In.59151, In.64014. Dimensions: 8–9 mm wing. Jackson colln.

Fig. 38 *Mesocixiella* (?) *fennahi* sp. nov. (Homoptera). **Holotype,** In.53942. R = rostrum, E = eye. Total length of insect including wings 5·9 mm.

Figs 39–40 Gen. et sp. nov. 1A (Heteroptera). Fig. 39, In.59137. Length overall 9 mm. Fig. 40, In.59128, forewing. Co = corium, M = membrane.

Fig. 41 Gen. et sp. nov. 2A (Heteroptera). In.59152. Length of body 5·4 mm.

Fig. 42 Gen. et sp. nov. 8A (Heteroptera). Bristol Museum specimen no. 111/1958. Arrow indicates metathoracic gland. Length of insect 32 mm.

When the Dorset pachymerids in the Jackson collection were examined, several possible new species were separated; these are listed below but although distinct from sp. nov. 3A, they are not sufficiently well preserved for description. All are from the Flatstones, Stonebarrow, Dorset.

Pachymeridiidae species 4A. Material: In.51028. Dimensions: 7·5 mm wing.

Pachymeridiidae species 5A. Material: In.51005. Dimensions: 6·7 mm wing.

Pachymeridiidae species 6A. Material: In.50999. Dimensions: 6·3 mm wing.

Infraorder **NEPOMORPHA**

Family **CORIXIDAE** Leach, 1815

Two specimens of aquatic corixid bugs are ascribed to this family but they are too poorly preserved to warrant a formal description and name.

MATERIAL. 2 specimens from Black Ven, Charmouth; In.59140, In.59166. Dimensions: 9–10 mm × 5 mm body. Jackson colln.

Family **BELOSTOMATIDAE** Leach, 1815

This family of aquatic bugs is represented by three specimens in the Jackson collection and one well-preserved specimen from the same Dorset locality in the City of Bristol Museum and Art Gallery. The Dorset specimens are the earliest known examples of the family, which was evidently well differentiated into a discrete group by the Lower Lias. Most of the specimens show the movable breathing siphon characteristic of this aquatic family.

Genus ***MESONEPA*** Handlirsch, 1906

TYPE SPECIES. *Mesonepa primordialis* Handlirsch (1906: 637), by subsequent designation of Popov (1971: 116). Jurassic, western Europe.

Mesonepa **species 7A**

DIAGNOSIS. Smaller than other species of *Mesonepa*.

MATERIAL. Two specimens from Stonebarrow, Dorset; In.51014, In.59383. Dimensions: 13 × 6 mm.

DISCUSSION. This is one of the smallest species known in the family but has many of the features typical of Recent species. The scutellum is broad and is a unique feature, suggesting that the earliest belostomatids may have resembled the naucorids.

Gen. et sp. nov. 8A

Fig. 42

DIAGNOSIS. Belostomatids with anterior tarsi and tibia not fused.

MATERIAL. One specimen from Charmouth, Dorset; in City of Bristol Museum and Art Gallery. Dimensions: 32 × 18·5 mm.

DISCUSSION. This species, which looks very similar at first glance to Recent species, differs in the structure of the forelegs. In Recent species the forelegs are modified into grasping organs and the tarsi and tibia are fused together. With this they seize their prey. In the new species the tarsi are free and not fused to the tibia and presumably a slightly different technique for grasping the prey was used. The preservation of the metathoracic gland (Fig. 42, arrowed) shows clearly, but the fact that some of the components were red as in modern species is even more remarkable. A preliminary examination of the contents of this gland has indicated a high sulphur level for the red material and may well indicate the presence of organo-sulphur compounds (see p. 112).

Order **RAPHIDIOPTERA**, snakeflies

Adults and larvae of this order are predatory, feeding on other insects. The Raphidioptera have a long fossil history but the Permian and Upper Carboniferous species which have been ascribed to the order are probably not correctly assigned (Carpenter 1967). There are only about 160 living species in the world, although Carpenter (1967) considered that they were a more diverse group in the Mesozoic. Most of the fossils are known only from the wings (e.g. Carpenter 1936, Martynova 1947, 1961, Macleod 1970) while the characteristically shaped body with elongate pronotum is rarely preserved. Although the exact shape of the prothorax is not clear in the first species described below, it is certainly somewhat elongated.

Family **MESORAPHIIDIDAE** Martynov, 1925*a*

DIAGNOSIS. Subcostal vein ends around the middle of the costal margin. Costal area narrower than in Recent Raphidioptera. Rs originated well before centre of wing.

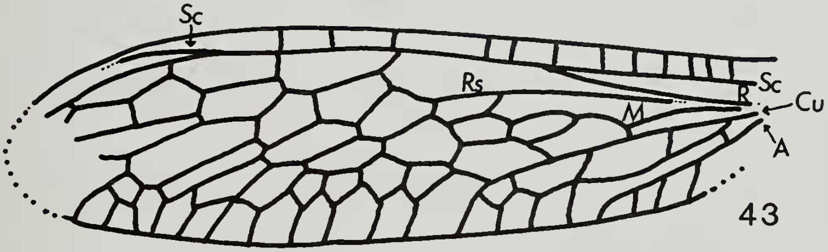
Lower and Upper Jurassic.

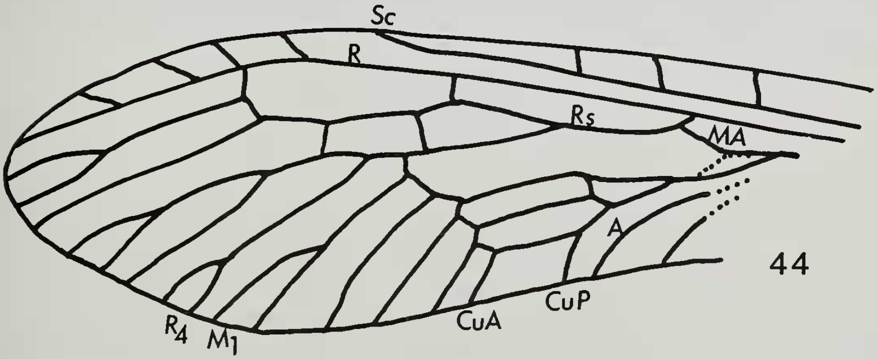
Genus *METARAPHIDIA* nov.

TYPE SPECIES. *Metaraphidia confusa* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Forewing with two large radial cells between R and Rs. Short pterostigmal cross-veins. Hindwing broadly similar, subcostal vein slightly shorter than in forewing.

NAME. Varied from *Raphidia*.





Figs 43–44 Diagram of wing venations in Raphidioptera. A = anal veins, Cu = cubital veins, M = median veins, MA = anterior median vein, R = radial veins, Rs = radial sector, Sc = subcostal vein. Fig. 43, *Priscaenigma obtusa* gen. et sp. nov. Fig. 44, *Metaraphidia confusa* gen. et sp. nov.

Discussion. The presence of pterostigmal cross-veins differentiates this genus from others in the Mesoraphidiidae. Pterostigmal cross-veins are also found in Recent Raphidiidae but the very elongate radial cells are characteristic of *Metaraphidia*. There are also more marginal branches (8–9) to the radial veins than in other genera of Mesoraphidiidae.

Metaraphidia confusa sp. nov.

Figs 44–45

Diagnosis. As genus. Discal cell small, less than half length of either radial cell.

Name. 'Mixed up'.

Description. Forewing with hairy costal margin, base of wing obscured. Rs branches off R towards base of wing. Base of M and origins of MA and MP obscured. MP short, probably fused for part of length with Cu. Posterior median cells all broadly similar in shape. Fore and hind wings overlying one another. No trace of pterostigma. Body and head partially obscured. Prothorax longer than width of head. Abdomen slender, tip enlarged.

Holotype. GSM 117552 (Fig. 45); Charmouth, Dorset; in British Geological Survey collection. Dimensions: Forewing 14·5 × 4·8 mm.

Discussion. This snakefly was evidently washed up against an ammonite and buried with it. Also trapped against the same ammonite was another insect; all three animals were fossilized together. The second insect, probably dipterous but poorly preserved, was fossilized partly under the snakefly (Fig. 45, A–D). Most of the ammonite (A) has been cut away to show the underlying insects, of which the dipterous wing (B) is just faintly visible next to the larger insect. The snakefly head (C) and prothorax (D) are just visible on the specimen but three of the four wings are tightly overlapped and individual details are difficult to discern. Fortunately one forewing is displaced slightly clear of the others.

Family **BAISSOPTERIDAE** Martynova, 1961

Diagnosis. Raphidians with a long or short Sc. Cells in radial and median area of wing more numerous than in Mesoraphidiidae.

Lower and Upper Jurassic.

Genus ***PRISCAENIGMA*** nov.

Type species. *Priscaenigma obtusa* sp. nov. Lower Lias, U.K.

Diagnosis. Raphidians with very long basal radial cell and 3–4 more radial cells to apex of wing. The long basal cell separates this genus from *Baissoptera* Martynova.

Name. 'Ancient riddle'.

Priscaenigma obtusa sp. nov.

Figs 43, 46

Diagnosis. As genus.

Name. 'Blunt'.

Description. Forewing, subcostal vein simple, reaching to near wing apex. One basal subcostal cross-vein present (but area distorted and others may be present), pterostigma obscure. M arising off R. Intramedian cell broader apically. CuA roughly parallel to hind margin with 1–2 apical branches. Several rather elongate cells in radial and median areas.

Holotype. In.53898 (Fig. 46); Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 12·6 mm long.

Discussion. This specimen has been fossilized with its wings together, and as a result it is difficult in one or two places to distinguish the underlying wing veins from those of the top

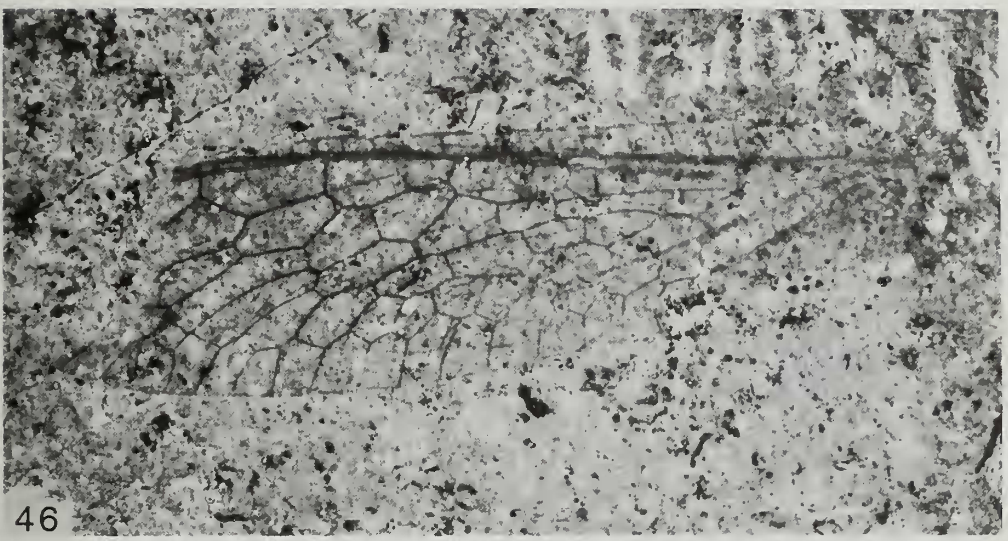


Fig. 45 *Metaraphidia confusa* gen. et sp. nov. (Raphidioptera). **Holotype,** British Geological Survey collection no. GSM 117552. Length of forewing 14·5 mm. The anterior part of the insect body was covered by an ammonite which has been partly removed; there is also a small dipterous specimen below this ammonite. A = ammonite, B = dipterous wing, C = head of *Metaraphidia*, D = protothorax of *Metaraphidia*, E = abdomen of *Metaraphidia*.

Fig. 46 *Priscaenigma obtusa* gen. et sp. nov. (Raphidioptera). **Holotype,** In.53898, forewing 12·6 mm long.

wing. In particular there is a short, indistinct, vein between the subcosta and the costal margin about half-way along the wing. This is almost certainly part of the underlying wing (? a hindwing) and not the subcostal vein of the fore (top) wing. The actual subcosta of the forewing appears to extend almost to the apex of the wing.

Initially this specimen was considered to be a chrysopid (Neuroptera), with some general similarities to the aberrant Recent genus *Kimochrysa* Tjeder, 1966 (Chrysopidae); in particular the long radial cell and the shape of the intramedian cell are similar. However, the origin of the radial sector is atypical of the Chrysopidae and the marginal veins in the fossil are unbranched. The cells in the median/apical area of the wing are more numerous than in the Mesoraphidiidae and are more typical of the Baissopteridae, although the described species of *Baissoptera* Martynova all have shorter subcostal veins. The radial cell in *Priscaenigma* is longer than in *Baissoptera* and the new species may well merit a new family of its own.

Order **MECOPTERA**, scorpion flies

The publication of their bibliography of the Mecoptera by Schlee & Schlee (1976) and of Willmann's (1978) catalogue of fossil Mecoptera has brought together the very scattered literature of this order.

Following Hennig (1981) and other workers, the two main suborders of the Mecoptera, Eumecoptera and Protomecoptera, are accepted here. The Protomecoptera, which are exclusively fossil, have many subcostal veinlets and a modified cubital vein. The vast majority of Recent and fossil species are placed in the Eumecoptera, in which the number of costal veinlets is reduced and the cubital vein is unbranched. Hennig interpreted the cubital vein as a composite one with M_4.

From the Lower Permian into the early Jurassic, Mecoptera fossils are common. They are known from the Lower Cretaceous and into the Tertiary (Willmann 1978) but are far less abundant in the Recent fauna. In the late Triassic and throughout the Jurassic fossil Mecoptera are numerous both as species and individuals, their abundance at this period contrasting sharply with the small size of the Recent fauna, with only about 300 extant species. This is the reverse of the position with, for example, the Diptera or Lepidoptera, which are rare as fossils in the Jurassic but abundant in the Recent fauna.

Recent Mecoptera are mostly carnivorous in adult and larval stages, feeding on insects. Mecoptera do not feed on the wing like dragonflies but hunt for their prey while it rests or feed on dead insects. There is no reason to suppose, from a study of the few preserved mouthparts of fossil Mecoptera, that their feeding habits were any different from those of their living relatives.

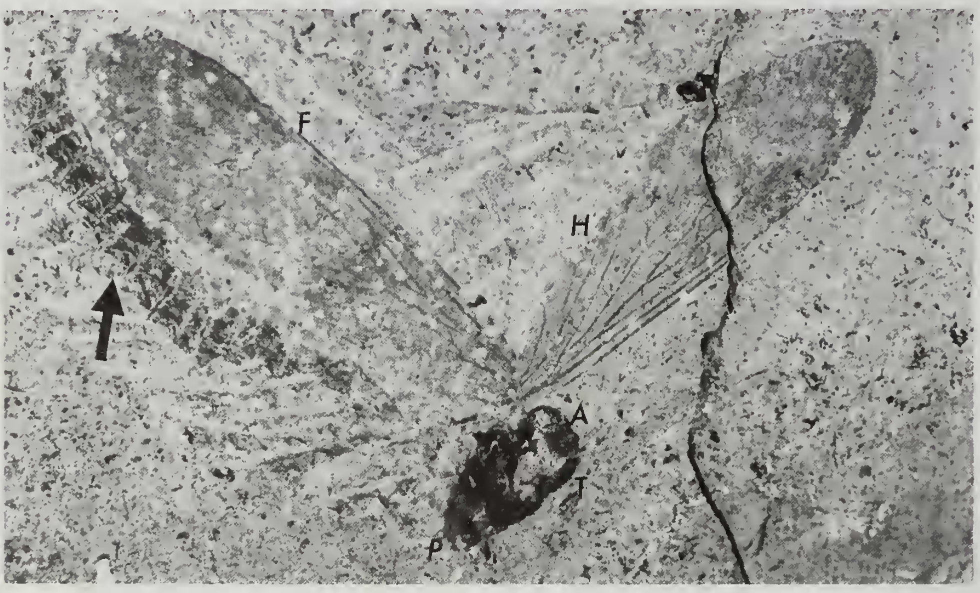


Fig. 47 *Orthophlebia capillata* sp. nov. (Mecoptera). **Holotype,** In.53924, part. A = anterior of thorax, P = posterior of thorax, F = forewing, H = hindwing, T = thorax. Arrow indicates chisel marks, not abdomen. See Figs 48, 51.

The classification of fossil Mecoptera is based mainly on small venational differences. These differences are used at both the specific and generic level but unfortunately we do not know how much intraspecific variation there is in these characters. Some of the finer points, such as the minor branching of veins near the wing margin, may well prove to be intraspecific. There are 15 specimens in the Jackson collection although several are represented by only small fragments. Three species are recognized.

Suborder **EUMECOPTERA**

Family **ORTHOPHLEBIIDAE** Handlirsch, 1906

DIAGNOSIS. Forewing with long subcostal vein reaching the pterostigma. Radial vein diverging from Sc with five or seven branches. Usually five medial veins.

This family is known from the Triassic to the Jurassic in Europe, Asia and Australia.

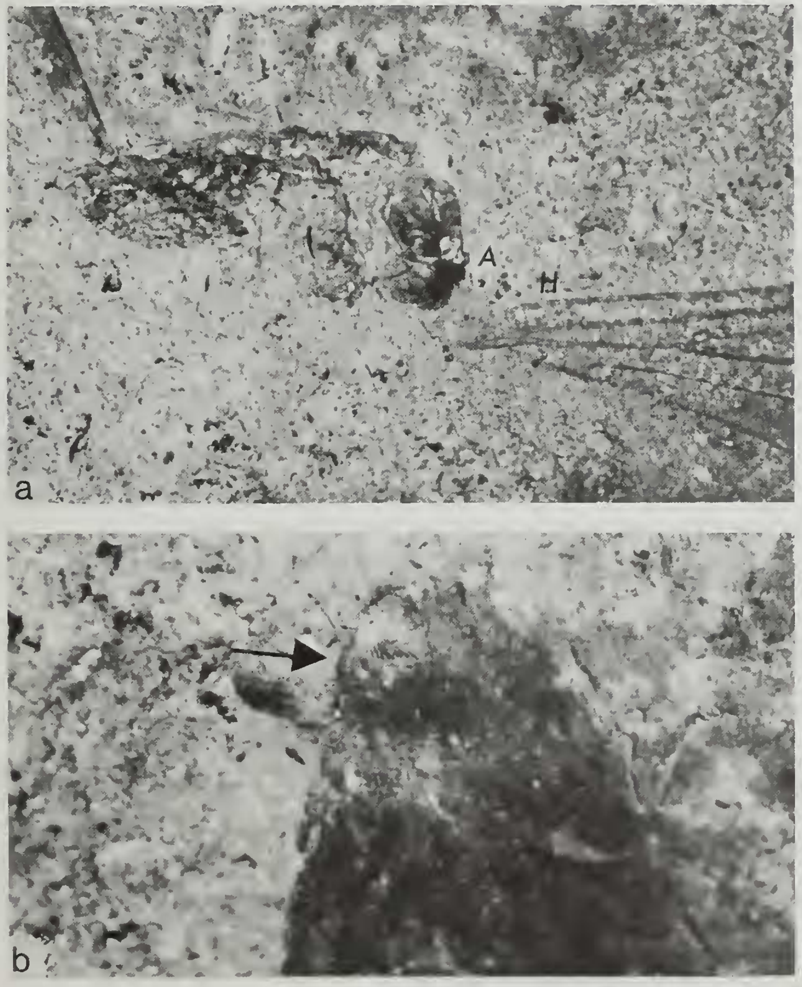


Fig. 48 *Orthophlebia capillata* sp. nov. (Mecoptera). **Holotype,** In.53924, counterpart. a, thorax, 7·5 mm long. A = anterior margin of thorax, H = hindwing base. b, posterior part of thorax to show setae (arrowed). See Figs 47, 51.

Genus *ORTHOPHLEBIA* Westwood, 1845

Type species. *Orthophlebia communis* Westwood (*in* Brodie 1845: 102), by subsequent designation of Tillyard, 1933. Upper Triassic and Jurassic of Europe and Asia.

Diagnosis. Orthophlebiids with six or seven branches to Rs.

Orthophlebia capillata sp. nov.

Figs 47–49, 51

Diagnosis. Large orthophlebid with curved Cu$_1$ in forewing joining Cu$_2$. Hindwing with Cu$_1$ and M joined. Veins of hindwing with Y-shaped 1A.

Name. 'Hairy'.

Description. Forewing, Sc reaches pterostigma; R$_1$ branches in pterostigma; Rs gives rise to seven final branches on wing margin. Anterior median vein has short branch near wing margin (M$_1$ + M$_2$) and a single M$_3$. M$_4$ and M$_5$ arise from a short postmedial vein. Cubital vein divides near base into curved anterior and straighter posterior branches. Three anal veins. Few cross-veins preserved. Whole wing covered with microtrichia with larger hairs along veins. Hindwing with humeral vein; seven-branched Rs. M with four branches and Cu$_1$ arising from near base of M. One cross-vein from CuP to 1A forms part of the distinctive Y-vein formed by 2A. Thorax partially preserved, with clear indication of setae (Fig. 48b), particularly eight post-dorsal setae on metanotum. Prothorax shorter than broad. Part of hind leg, femur 5 mm long, covered with short hairs.

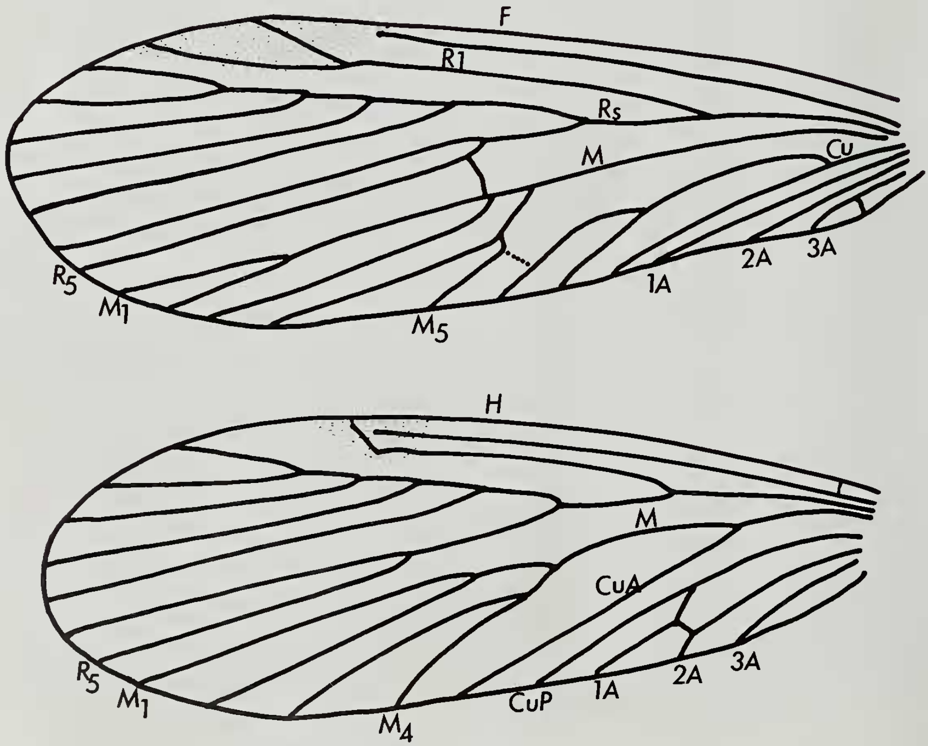


Fig. 49 *Orthophlebia capillata* sp. nov. (Mecoptera). Diagram of wing venations; F—forewing, H—hindwing. A = anal veins, Cu = cubital veins, M = median veins, R = radial veins.

HOLOTYPE. In.53924 (Figs 47–49, 51); Flatstones, Stonebarrow, Dorset; part and counterpart. Jackson colln. Dimensions: Forewing length 24 mm, width 6·3 mm. Hindwing, 21·5 × 6 mm.

PARATYPES. In.49579, In.49601, In.53899, In.59380.

DISCUSSION. The new species from Dorset, with a wingspan of 50 mm, is larger than any other species of *Orthophlebia* except the huge *O. grandis* Martynov 1927, from Turkestan, which has a wingspan of 70 mm. Even *O. gigantea* Tillyard, from the Trias of Strensham (U.K.), had a wingspan of only 38 mm and most Liassic species were much smaller.

All the specimens of *O. capillata* show the very hairy nature of the wings, with hairs on the membrane as well as along the veins. In.53899 shows the microtrichia particularly well when the rock surface is wet; some larger hairs are preserved on the membrane while even larger setal bases are clearly visible along the anal veins: presumably there were originally long setae on these veins. The costal margin is covered with short stout hairs, while the pterostigma is covered by a dense patch of microtrichia. The wing membrane as preserved in some specimens looks as though it may have been slightly thickened and perhaps translucent in life.

The smaller *O. anglicus* described from the Lower Lias of Gloucestershire lacks the Y-shaped second anal vein present in the hindwing of *O. capillata*.

Genus *PROTORTHOPHLEBIA* Tillyard, 1933

TYPE SPECIES. *Protorthophlebia latipennis* Tillyard (1933: 28), by original designation. Upper Trias to Upper Jurassic, Europe and Asia.

DIAGNOSIS. Orthophlebiids with a wing length of less than 10 mm. Rs five-branched.

Protorthophlebia latipennis Tillyard, 1933

Figs 50, 52–53

1933 *Protorthophlebia latipennis* Tillyard: 29, fig. 6.

DIAGNOSIS. As genus. Three anteradial veins; setal bases on anal veins large and prominent.

DESCRIPTION. Sc and R_1 end at pterostigma. R_2 forked near wing margin. Two-branched MA, three-branched MP. Three anal veins; CuA curved joining CuP near base. Long hairs on Sc, R, and M at the base, large setal bases on anal veins. Whole membrane covered with short, fine hairs with short, stout hairs along costal margin.

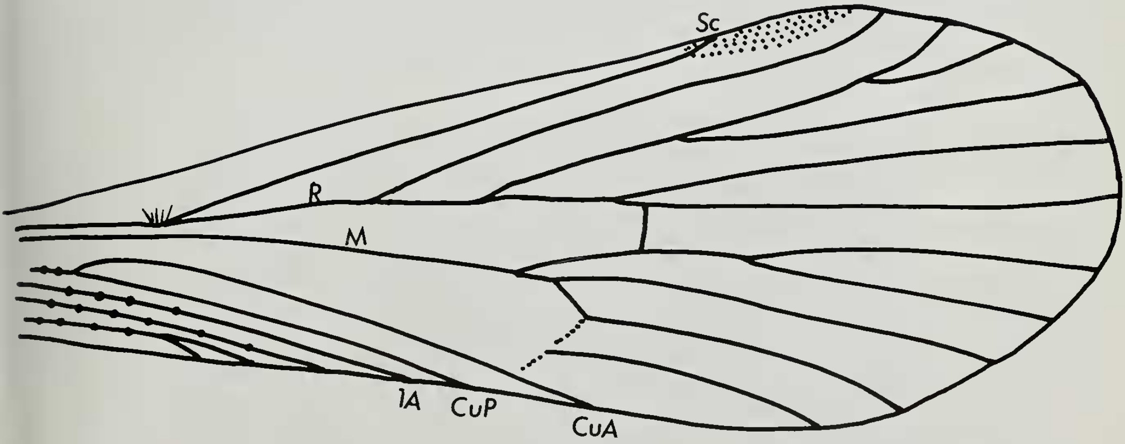
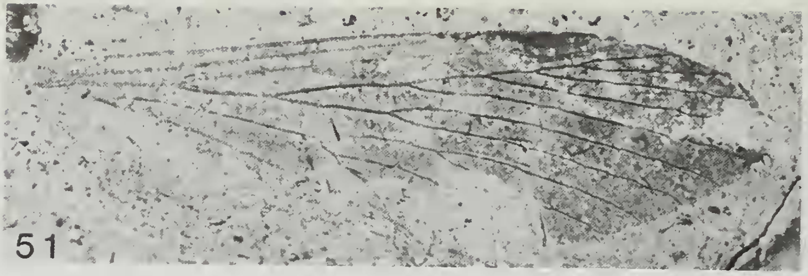


Fig. 50 *Protorthophlebia latipennis* Tillyard (Mecoptera). Diagram of wing venation. A = anal vein, M = median vein, Cu = cubital vein, R = radial veins, Sc = subcostal vein.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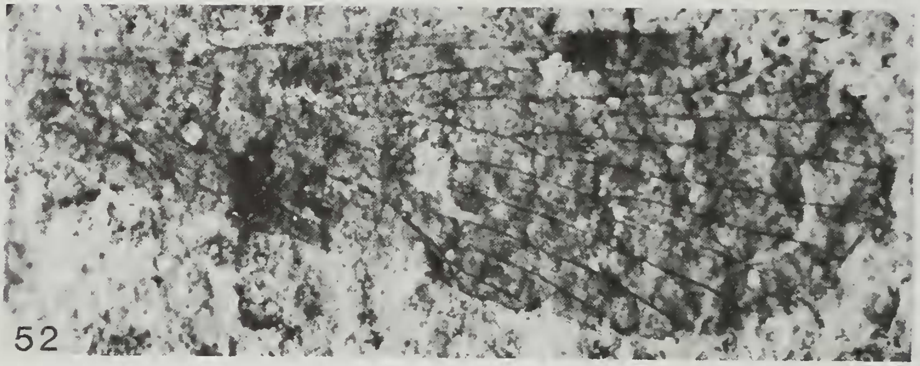
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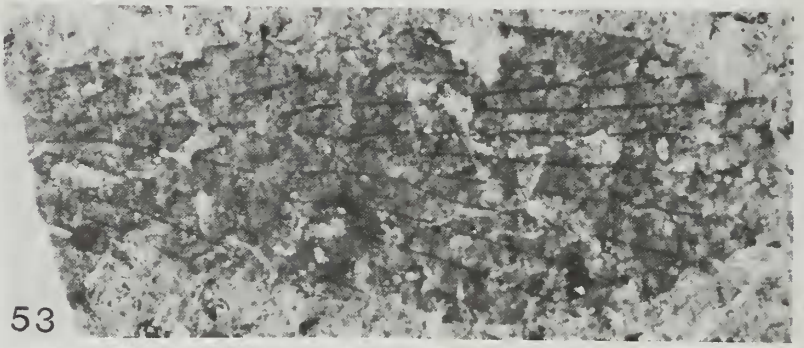
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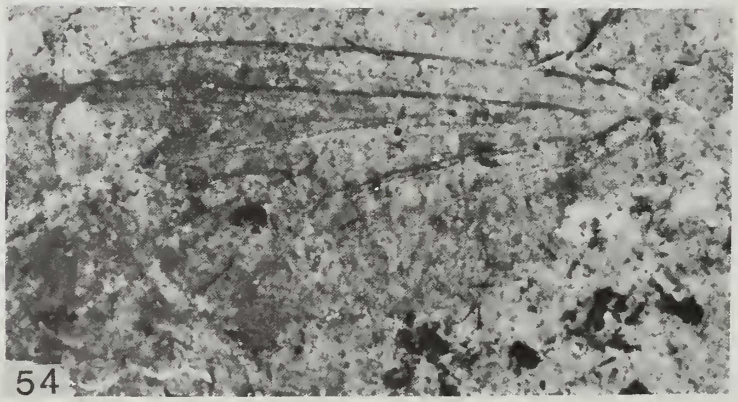
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HOLOTYPE. I.11746; Lower Lias, Binton, Warwickshire. Rev. P. B. Brodie colln., purchased April 1898. Dimensions: Length 9 mm, width 3 mm.

OTHER MATERIAL. In.49575, ? In.53954 (Fig. 53), In.53963, In.59120, ? In.59365, In.59371, In.59384 (Fig. 52). Charmouth, Dorset. Jackson colln.

DISCUSSION. Although there are some minor venation differences between the holotype from Warwickshire and the Dorset specimens, most of the venation is very similar. The holotype has a forked vein at the apex of M_1 while this is a single vein in the specimens from Dorset. The holotype is slightly broader in proportion to its length than the Dorset specimens, but is spread out on fine-grain rock while the Dorset rock is coarser and many of the wings are slightly folded: see below. This would certainly be enough to account for the small differences between the specimens.

There is also a stratigraphical difference between the Dorset and the Warwickshire specimens; the holotype is from the older Planorbis Zone of the Lower Lias, while the Dorset material is from the Obtusum Zone.

The presence of a thyridium, represented by the less sclerotized parts of the veins, is indicated by less clearly defined veins at the base of the primary fork of the median vein; it was presumably a flexion line. The large setal bases on the anal veins of the forewing would have had stout setae on them in life, the wings were covered in hairs, and the whole insect probably looked broadly similar to Recent Trichoptera. The strongly curved anterior cubital joining the postcubital near the base is diagnostic of this species. Few cross-veins are preserved, although r-m is clear in one specimen. Specimen In.59120 is slightly damaged and the median veins near the wing margin are not as clear as in others; only four median branches can be traced, although the fifth can just be discerned. In.53954 (Fig. 53) is a slightly larger specimen than the others and is only provisionally placed here.

Family **PSEUDOPOLYCENTROPODIDAE** Handlirsch, 1906

This family formed part of the Paratrichoptera according to Martynov (1927), Tillyard (1935) and Rohdendorf (1962, 1974), but the Paratrichoptera are now considered an early specialization nearer, but not in, the stem-group of the Diptera (Hennig 1981), while the Pseudopolycentropodidae are now placed in the Mecoptera (Willmann 1978). The species currently included in the family are from the Upper Lias or Upper Jurassic of continental Europe; none have previously been reported from the Lower Lias.

Genus ***PSEUDOPOLYCENTROPUS*** Handlirsch, 1906

TYPE SPECIES. *Phryganidium perlaeformis* (Geinitz 1884), by monotypy (Handlirsch 1906: 482). Jurassic, Europe.

DIAGNOSIS. Wing broader in apical third. Sc short; R_1 relatively straight. M five-branched.

Pseudopolycentropus prolatipennis sp. nov.

Figs 55–56

DIAGNOSIS. As genus. Median cell distinct.

NAME. *Pro* + *latipennis* (an existing species).

DESCRIPTION. Wing broadly triangular with oblique outer (terminal) margin. Pterostigma present at apex of R_1, almost reaching to R_2. Rs and R_2 diverge sharply with anterior and

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Fig. 51 *Orthophlebia capillata* sp. nov. (Mecoptera). **Holotype,** In.53924, counterpart, hindwing. See Figs 47, 48.

Figs 52–53 *Protorthophlebia latipennis* Tillyard (Mecoptera). Fig. 52, In.59384, forewing, 9 mm long. Fig. 53, In.53954, forewing provisionally placed in this species.

Fig. 54 *Prodocidia spectra* gen. et sp. nov. (Diptera). **Holotype,** In.49226, wing, 7 mm long.

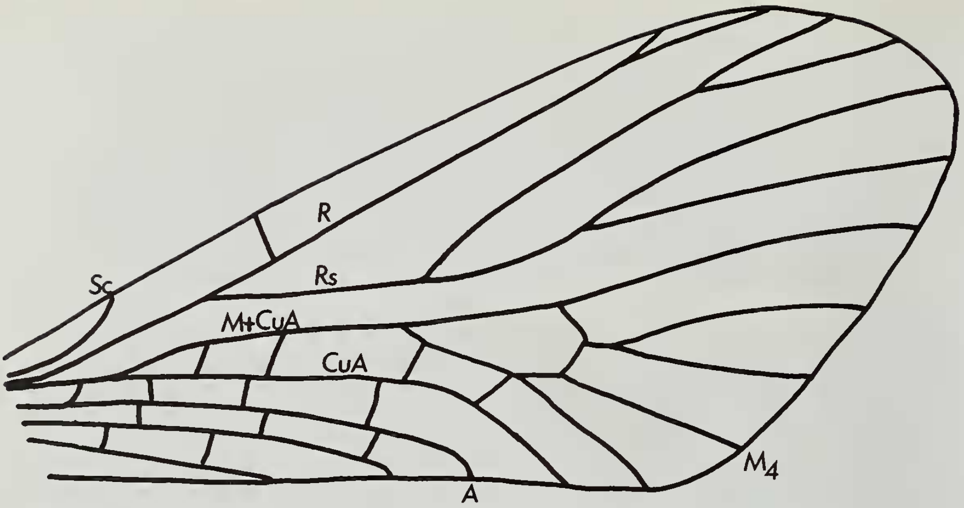


Fig. 55 *Pseudopolycentropus prolatipennis* sp. nov. (Mecoptera). Diagram of forewing venation. A = anal veins, Cu = cubital veins, M = median veins, R = radial veins, Rs = radial sector, Sc = subcostal vein.

posterior branches of R_2 and R_3 curved. Posterior branch from Rs into R_4 and R_5. Five median veins, stem of M curved at base, joining Cu for a short distance before separating median cell formed by anterior and posterior of median vein with M_2 and M_3 on a common stalk. Cu separated from base of M by slightly curved, oblique vein. CuP absent. Three anal veins, unbranched. Single cross-vein visible in costal area just before middle, other cross-veins not visible (? absent) except for anal and cubito-anal areas where they are well developed. Wing veins and membrane hairy with large setal bases along anal veins.

HOLOTYPE. In.53915 (Fig. 56); Woodstones, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 6·3 × 3 mm.

DISCUSSION. *P. prolatipennis* at 6·3 mm long is smaller than *P. latipennis* (8 mm), and has more cross-veins in the anal area. However, the cross-veins are extremely difficult to see and this may be a preservational difference. *P. latipennis* Martynov was found in the Upper Jurassic of Karatau and is similar in shape to the Dorset specimen; both species have the same curious fusion of the median with the cubital vein for a short distance near the base. The membrane of *P. prolatipennis* has preserved very darkly on the rock and may well have been opaque in life.

The family Pseudopolycentropodidae is a curious group with a strongly reduced subcostal vein and the basal vein fusions already mentioned. Martynov (1927: 665) regarded the family as closely allied to the Diptera, 'representing a side-stem, which arose, together with the Diptera, from some unknown Mecopteran ancestor of small size'. The number of anal veins in the suborder Paratrichoptera, to which *P. latipennis* was attributed by Rohdendorf (1962), was regarded as characteristic of the suborder and was given as one or two (1962: 292). This was based on the way the veins join near the base of the wing and assumed that, while the median vein went directly to the base of the wing after joining the cubital, the latter continued along the cross-vein and then ran to the base of the wing. This meant that the rest of the vein was part of the cubital system and was regarded as a postcubital. However, if this latter vein ('CuP') is considered the first anal, then CuP is actually absent. Evidence to support the absence of CuP is shown by the presence of similar small setal bases on each of the 'three' anal veins, whereas these types of setal bases are absent from the anterior cubital vein. It is unusual for the cubital to join with the first anal vein, but not impossible.

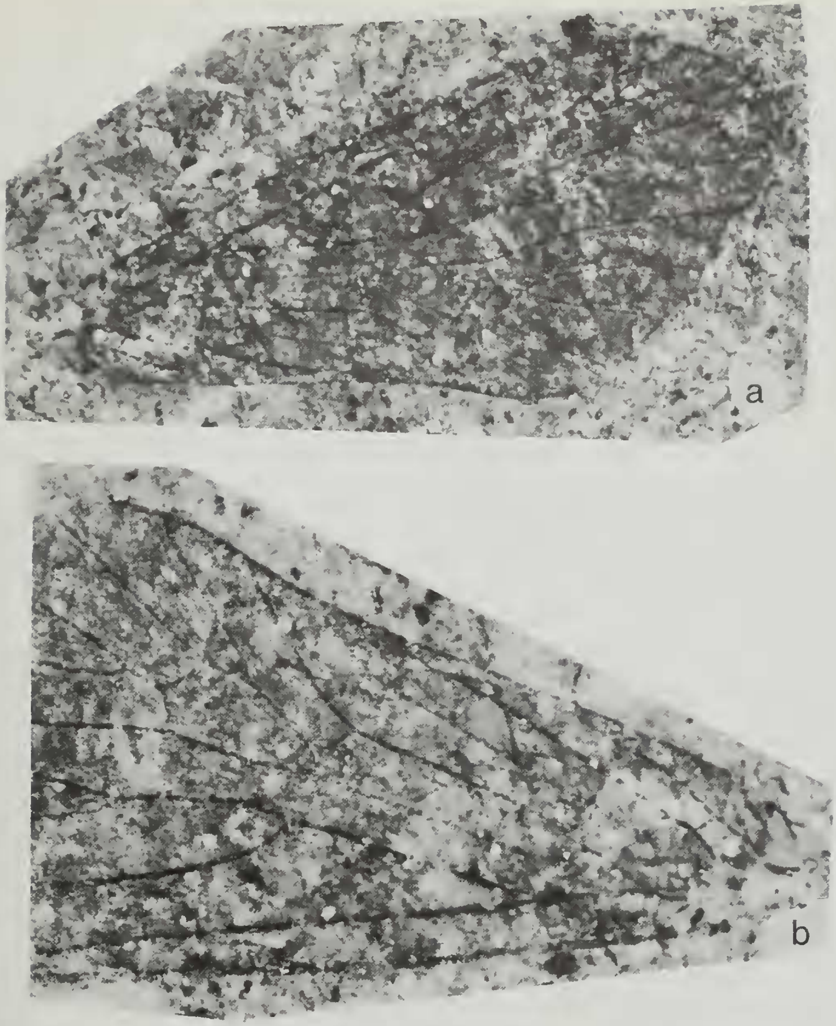


Fig. 56 *Pseudopolycentropus prolatipennis* sp. nov. (Mecoptera). **Holotype,** In.53915. a, part, forewing, 6·3 mm long. b, counterpart, basal area of wing.

The exact interpretation of these veins will have to await discovery of more specimens in this and related genera. Certainly the wing is highly specialized, with the reduced subcostal vein forming a small 'costal brace' and a distinct strengthening of the wing by the formation of the medial cell to take account of the changed shape of the wing. *P. prolatipennis* can be regarded as a highly specialized Mecopteran and unlikely to have been the direct ancestor of any modern order. However, it does show various wing modifications and venation specializations indicating how the development of the modern Diptera–Lepidoptera types may have evolved. The fossil record of the Pseudopolycentropodidae suggests that the group was widespread across Europe and Asia in the Mesozoic.

Order **DIPTERA**, two-winged flies

Only a single wing in the Jackson collection is clearly dipterous, although one other, possibly dipterous, was found closely associated with an ammonite and a species of Raphidioptera (p.

148; Fig. 45). Diptera are rare in the early Jurassic (Rohdendorf 1974, Kovalev 1982) and any specimen which can be recognized, even if only to the Order Diptera, deserves a detailed analysis. The Lower Lias specimen is damaged at the wing apex and part of this is torn and folded over. The posterior wing margin is indistinct and Fig. 57 shows the extent of the visible wing membrane; this is probably reasonably near the actual wing margin. There is a series of brown veins, mostly with fine hairs, as well as raised veins or folds in the wing which are not coloured. The wing has a straight radial vein (R_1) and the radial sector and median veins run close together and are virtually inseparable for part of their length. It is possible that the wing membrane may be slightly folded which would account for the approximation of the radial sector and median veins. The cubital vein is thick and double with the postcubital not reaching the wing margin. The anal area was probably relatively large, judged from the extent of the preserved wing membrane, but only one anal vein is present.

Suborder **NEMATOCERA**

Superfamily **BIBIONOMORPHA**

Family **MYCETOPHILIDAE** Macquart, 1838

The new genus described below is only provisionally placed in this family. Whilst it broadly resembles Recent *Diadocidia* Ruthe (which is sometimes placed in its own family, Diadocidiidae), the larger family Mycetophilidae *sens. lat.* is preferred. The fossil species is placed within the broad division of fungus-gnats (Fungivoridea, auctt.) and probably should be placed in a family of its own.

Genus ***PRODOCIDIA*** gen. nov.

TYPE SPECIES. *Prodocidia spectra* sp. nov. Lower Lias, U.K.

DIAGNOSIS. Sc long, reaching almost to apex of wing. Pterostigma present. Rs and M run close together. Cell elongate. The long subcostal vein separates this genus from the rest of the Fungivoridea of Rohdendorf.

NAME. Greek *προ* + *δοκίδιον*, a small shaft.

Prodocidia spectra sp. nov.

Figs 54, 57

DIAGNOSIS. As genus.

NAME. 'Images in the mind'.

DESCRIPTION. Apex of wing damaged; exact extent of all wing margin indeterminate but dotted line in Fig. 57 shows extent of preserved membrane. A broad wing, humeral vein near base of subcosta. R_1 simple, Rs arises towards base of wing and runs close to M. Probably two apical branches to Rs. M with two apical branches, m-cu cross-vein distinct, forming part of elongate cell. Cubital cell double along hind margin of cell, Cu_1 continues to wing margin. Strongly curved, single, anal vein. Costal vein with fine hairs, macrotrichia on wing base.

HOLOTYPE. In.49226 (Fig. 54); Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Length 7 mm.

DISCUSSION. The length of the subcostal vein, almost reaching the wing apex, distinguishes this species from most fossil fungus-gnats (Fungivoridea, auctt.) and also from Recent species of *Diadocidia*. Apart from the length of the subcostal, the rest of the venation is similar to a group of Recent genera of fungus-gnats, including *Diadocidia*, *Symmerus* Walker and *Ditomyia* Winnertz (McAlpine *et al.* 1981). The cell in *P. spectra* is well marked and elongate, and the pterostigma is marked by numerous microtrichia. Fungus-gnats have been recorded from the Triassic and Jurassic rocks of the U.S.S.R. (Rohdendorf 1962) and are widespread and abundant at the present day.

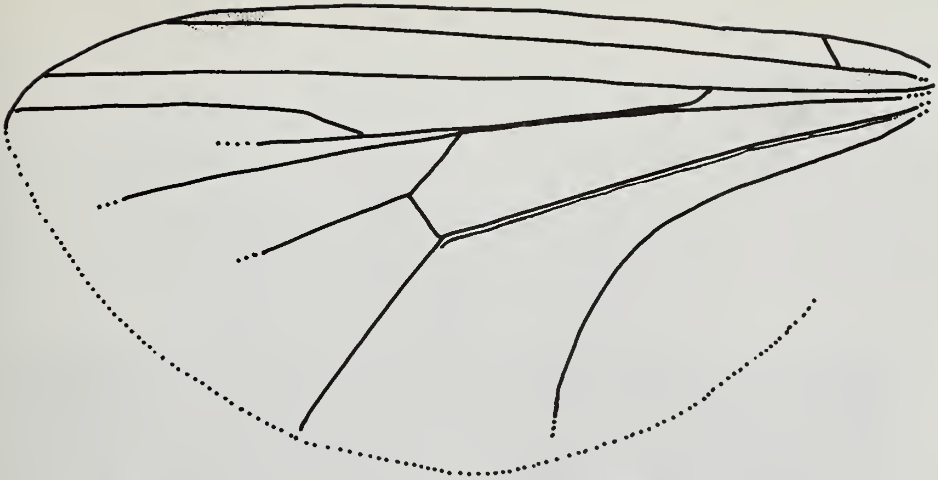


Fig. 57 *Prodocidia spectra* gen. et sp. nov. (Diptera). Diagram of wing venation.

Order **LEPIDOPTERA**, butterflies and moths

When a piece of Dorset Lias, collected by Jackson, was recently split it revealed a small scale-covered wing. This discovery has significance in the continuing debate on the evolution of the Lepidoptera, to which the fossil is attributed. There is no other direct evidence of scale-covered wings earlier than the Upper Jurassic, 40–50 million years later (Rasnitsyn 1983). It is important, therefore, to give careful consideration to the systematic position of this fossil.

The earliest recognized scale-covered wings of Lepidoptera are from the Upper Jurassic (Rasnitsyn 1983) and the Lower Cretaceous, where a moth was found in Lebanese amber (Whalley 1978). Other, unassociated, scales were also found in this amber; on the basis of the specimen and the isolated scales two families of Lepidoptera, Micropterigidae and Incurvariidae, were recognized. Riek (1976) and Tindale (1980) described wings they consider lepidopterous from the Upper and Middle Trias respectively but these do not have any preserved scales.

Although scales are characteristic of Lepidoptera, they are not exclusive to them and are also found in the Psocoptera, Diptera, Coleoptera and Trichoptera amongst the winged insects. From a study of these groups only the Amphiesmenoptera (Lepidoptera + Trichoptera and their stem-group; Kristensen 1975) are considered to have characters that occur in the fossil wing.

Family **ARCHAEOLEPIDAE** nov.

Diagnosis. Scale-covered wing with prominent forked cubital vein. Vein R_1 forked at apex. Scales with longitudinal ridges and few cross-ribs (trabeculae, Imms 1970). Radial vein four-branched; median three-branched.

Discussion. The family is separated from the Micropterigidae by the wing venation, particularly the anal veins. At present known from one wing, probably a hind wing. Lower Lias, U.K.

Genus ***ARCHAEOLEPIS*** nov.

Type species. *Archaeolepis mane* sp. nov.

Diagnosis. As family. Subcostal vein probably simple, 1A and 2A probably joined.

Name. 'Ancient scale'.

Archaeolepis mane sp. nov.

Figs 58–60

Diagnosis. As family.

Name. ‘Dawn’.

Description. Heavily scaled (? hind) wing. R_1 forked at apex, Rs forked, probably with third fork though origins obscure. Three median veins, obscure towards base. Cu clearly divided. 1A and 2A probably join; tip of 3A and rest of anal area indistinct. Scales 0·20–0·23 mm long, 0·06–0·08 mm wide. Strongly ridged, ridges vary in width, according to the width of scale, usually 0·002 mm apart. Cross-ribs mostly absent, although some lateral connections between

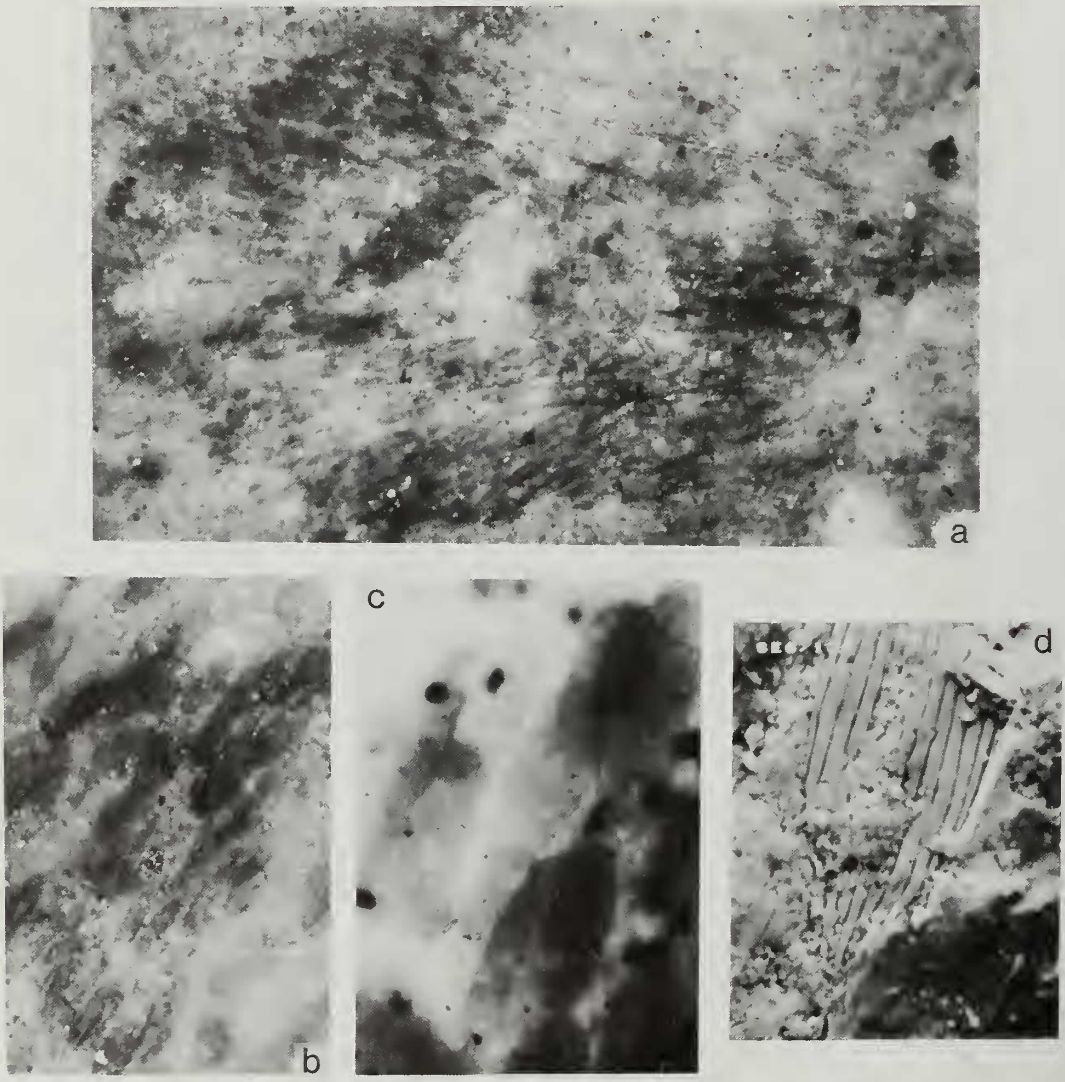


Fig. 58 *Archaeolepis mane* gen. et sp. nov. (Lepidoptera). **Holotype,** In.59397. a, wing, 5·3 mm long. b, wing scales, length of scales 0·20–0·23 mm. c, wing scales under ultra-violet light. d, stereoscan micrograph of uncoated wing surface, showing scales; magnification *c.* × 2000.

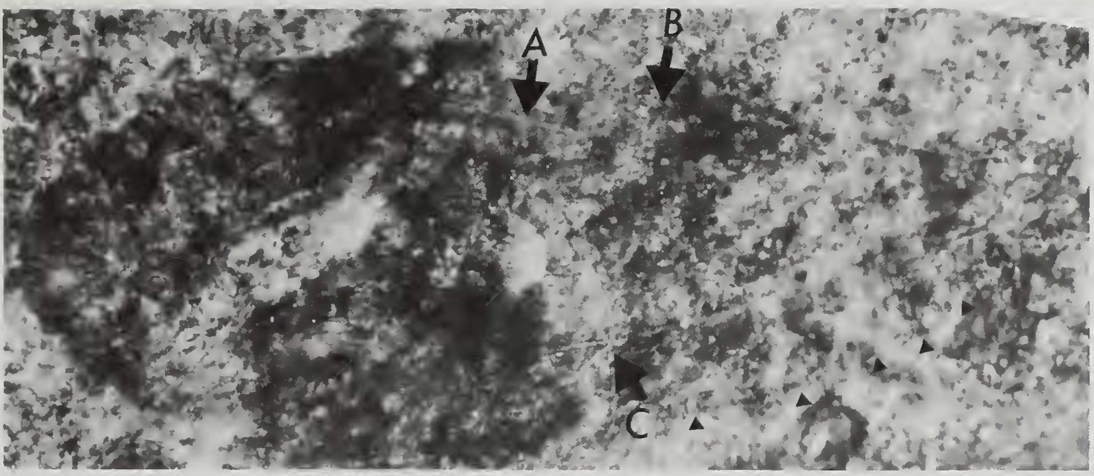


Fig. 59 *Archaeolepis mane* gen. et sp. nov. (Lepidoptera). Holotype, In.59397, whole wing under ultra-violet light. A = radial vein, B = subcostal vein, C = cubital fork. Small arrowheads indicate extent of hind margin of wing in anal area.

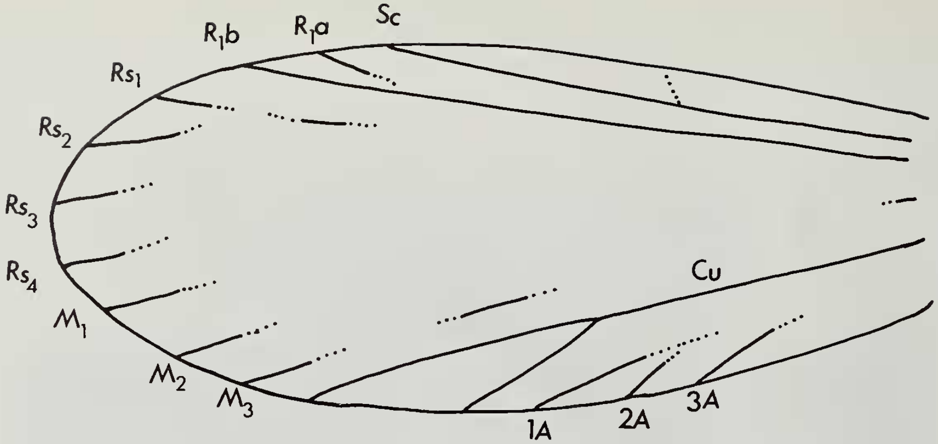


Fig. 60 *Archaeolepis mane* gen. et sp. nov. (Lepidoptera). Composite diagram of wing venation. A = anal veins, Cu = cubital vein, M = median veins, R = radial vein, Rs = branches of radial sector, Sc = subcostal vein.

the longitudinal ridges are apparent near base of some scales. Apex of scales smoothly rounded. Two, possibly more, different types of scales. Marginal scales thinner, some thinner scales mixed in with thicker ones on wing membrane. The wing margin has longer scales along the hind margin and probably had a substantial fringe of scales. Fewer ridges on some scales, 12–13 as against 18–22 on others. The ridges on the scales as seen in the stereoscan micrographs (Fig. 58d) are considered to represent the infilling between the original ridges (striae) and their compression, with the dark lines representing the ridges from the original scale. The scales shown in the micrographs are the narrow ones with fewer striae.

HOLOTYPE. In.59397 (Figs 58–59); Birchi nodules, Lower Lias, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: Length 5·3–5·6 mm, width 2 mm.

DISCUSSION. Although Lepidoptera or Trichoptera are the most obvious orders for the fossil wing, others cannot be eliminated without further consideration. Indeed some of the Recent scaly-winged Lepidopsocidae (Psocoptera) look superficially very similar to the Dorset fossil. Apart from these, consideration was also given to the possibility that the wing represented an extinct, scale-winged mecopteran (*sens. lat.*). Several families in the broad assemblage Mecopteroidea (Willmann 1978) have been considered as giving rise to the modern Diptera, Trichoptera and Lepidoptera (Tillyard 1933). Many Jurassic Orthophlebiidae have an unbranched cubital vein, contrasting with *Archaeolepis*, and are really early Mecoptera. The Pseudopolycentropodidae, which have a highly specialized and slightly lepidopterous wing shape, are also still considered Mecoptera (Willmann 1978). All these are known from the same deposit as *Archaeolepis*. Many of the fossil orthophlebiids from the Jurassic have the hairs clearly preserved on the wings but none are known with vein M_4 absent (as in the fossil). Although the Order Mecoptera was more diverse in the Mesozoic there are no living representatives with scale-covered wings, as there are for the other orders discussed below.

PSOCOPTERA. This order is known from the Permian and there are two Recent families, the Amphientomidae and Lepidopsocidae, which have completely scale-covered wings (Enderlein 1906). The psocid wing differs from *Archaeolepis* in venation, with Sc and R not running parallel and Cu unbranched. Some of the scales are toothed at the apex but the underside differs from lepidopterous-type scale with thickened ridges running transversely across the scale. In some of the fossil species of *Permopsocus* Tillyard, Cu is forked but Sc and R do not run parallel as in *Archaeolepis*. Thus the fossil *Archaeolepis* can be ruled out of the Psocoptera.

DIPTERA. Scales are present on the wing of many nematoceran Diptera and in the Psychodidae the wings are completely clothed with hairs and scales. In most Diptera, the scales, when present, are restricted to the veins although in the Cecidomyiidae the scales may cover the wings. In *Psychoda surcoufi* Tonnoir the wing is covered with long hair-like scales which are elongate and have a distinctly serrate edge, very similar to the elongate hairs of the Trichoptera. The scales in *Archaeolepis* are larger and their arrangement on the wing is different from Diptera of comparable size. Comparisons have been made with the scales of Recent mosquitoes, which are broadly similar but the venation and anal area are different. The scales on most mosquitoes are arranged along the veins. The fossil wing is not considered dipterous.

TRICHOPTERA. While the majority of Recent species have hairy wings, most of the families of the Suborder Integripalpia have a few species where the wings are covered in scales. These scales vary in shape and size and when studied under the stereoscan electron microscope cross-ribs can be seen. In the sister-group of the Integripalpia, the Suborder Annulipalpia, the wings are hairy and scales are not developed. Hennig (1981) commented that it is virtually impossible to separate the Lepidoptera and Trichoptera on wing venation alone. Probably the only apomorphic character in the wings of Lepidoptera is the fusion of M_4 with CuA, leaving, in effect, only three medial veins, as shown by *Archaeolepis*. Kristensen (1984) points out that M_4 is present in the fore (and some hind) wings of Lepidoptera Aglossata. While the scales on the wings of some Trichoptera are quite dense, they are frequently smaller than in Lepidoptera and do not usually give the overlapping cover typical of Lepidoptera.

LEPIDOPTERA. Although other lepidopterous groups, such as the Heterobathmiina, have been considered, the comparison of *Archaeolepis* is better made with the more primitive group Micropterigidae (Kristensen 1979) and more especially with species of *Sabatinca* Walker. A complete scale-covering of the wing is typical of the Micropterigidae and is similar to *Archaeolepis*. The shape and such venation as is preserved in the fossil is mostly consistent with the hind wings of Micropterigidae, and this, together with the forked cubital vein, is not inconsistent with the stem-group Amphiesmenoptera. Under the stereoscan the scales of *Archaeolepis* show a virtual absence of cross-ribs, a condition similar to the Micropterigidae and Eriocraniidae (Kristensen 1970). The subcostal vein in the fossil may be simple, the base is not clear and the radial fork (R_1a, R_1b) is similar to species of *Sabatinca*. The exact number of median veins in *Archaeolepis* is difficult to determine but there are probably three branches as in the Micropterigidae. If lepidopterous, then *Archaeolepis* is either the sister-group of the Zeugloptera (Micropterigidae) or of the Zeugloptera + Glossata + Heterobathmiina + Aglossata. Without further data neither this, nor even the position of *Archaeolepis* within the Lepidoptera itself, can be resolved.

In a recent paper Rasnitsyn (1983) reported traces of scales on a small insect from the Upper Jurassic of the U.S.S.R. He proposed a new suborder of Lepidoptera (Eolepidopterigina) and new family (Eolepidopterigidae) for the specimen, which he described as *Eolepidopterix jurassica*. No apomorphic characters were indicated to confirm the lepidopterous nature of the specimen nor did he say how it differed from scaly-winged Trichoptera. For the present I do not propose to place my new family, Archaeolepidae, in his new suborder but I certainly regard his evidence as showing that *Eolepidopterix* is lepidopterous.

Archaeolepis extends the age of these scale-winged insects back a further 45–50 million years, and new origins will have to be sought for the Lepidoptera in the Upper Triassic, as suggested by Riek (1976), or even the Middle Triassic (Tindale 1980). Probably the most important implication of *Archaeolepis* is not so much in the overall picture of the antiquity and evolution of the Lepidoptera, but in the Lepidoptera–plant relationship. Currently Lepidoptera are considered to have arisen at about the time of the earliest angiosperm (i.e. Upper Jurassic–Lower Cretaceous; Hughes 1976), and to have paralleled their evolutionary diversification. The latter is certainly true but it now appears that the scale-winged insects arose well before the earliest angiosperm. There is, however, no need to link the earliest Lepidoptera with angiosperms because many Recent lepidopterous larvae are capable of feeding on a wide range of non-angiospermous plants. This fact, however, is not proof that their ancestors did, since it might be a secondary habit. The existence of *Archaeolepis* well before the earliest angiosperm is more convincing evidence that early lepidopterous larvae probably did *not* feed on angiosperms. There were undoubtedly sources of pollen or spores for the adult food, as used by adult moths in the Recent Micropterigidae. Sources of liquid food, extra-floral nectaries, plant exudates etc., were available before the angiosperms and although the development of a lepidopteran-type proboscis cannot be entirely ruled out there is no evidence for its development in the Lower Jurassic. An analogy is therefore drawn between the pollen-feeding habits of modern adult Micropterigidae and the possibility that a similar method was available to *Archaeolepis*.

What is indisputable is that, in the Lower Jurassic, there were small moth-like insects with scale-covered wings. The delicate nature of the *Archaeolepis* wing suggests that it was not transported very far before fossilization, suggesting the site was near to a land mass.

Order **COLEOPTERA**, beetles

Beetles are the most abundant insects in the Dorset Lias, forming over 39% of the total insects found. This not only shows their undoubted abundance in the fauna from which the deposits were derived but also is a reflection of the durability of the toughened beetle elytra. Beetles are usually very strongly sclerotized with the elytra particularly tough in most cases. Up to 40% of the beetle fossils are represented by both elytra (as well as other parts) while in other orders fewer than 10% of the insects are represented by both forewings, even in groups where the forewings are more sclerotized than the hindwings (Orthoptera, Blattodea). For some reason the elytra from a single individual beetle were less likely to be separated than the forewings of other orders.

It is difficult, in many cases impossible, to place a single elytron (or even a pair of elytra) into a modern family reliably. The lack of venation in the elytra, which is used to identify the family in many other orders, is not compensated for by the increased sculpturing; the latter is sometimes a guide to the family but frequently elytral sculpturing is of no use on its own at the family level. Where a single elytron can be associated with a family (usually after consultation with a Coleoptera specialist), this has been given; the remaining unassociated elytra, which are often very distinctly patterned, are associated in species groups. This gives some indication of the diversity of the fauna, since they are associated on shape, size and the sculpturing of the elytra. An estimate of the total number of different species groups is considered to represent an approximation of the number of species of beetles. From this it is estimated that there are not fewer than twenty, and probably at least thirty, distinct species of beetles in the Dorset Lias. Comparison of these 'species' has been made with the beetle faunas described by Ponomarenko (1969) and Arnoldi (1977) from the Mesozoic of the U.S.S.R.

Family **ELATERIDAE** Leach, 1815

Genus ***ELATERINA*** Gardiner, 1961

TYPE SPECIES. *Elaterina liassica* Gardiner, by original designation (Gardiner 1961: 87). Lower Lias, U.K.

Elaterina liassica Gardiner, 1961

This genus and species were based on a single elytron found in the orbit of a fish during acetic acid preparation. The elytron, incomplete and in poor condition, has few details preserved. There is a distinct 'rim' along one side but the striae are barely visible. There is nothing left on the specimen to indicate that it is an elaterid beetle, and its elytra at 12·5 mm are longer than in any other Elateridae from the British Lias. It has not been possible to recognize this species from the many new specimens collected in the same locality but one specimen, In.59369, which has roughly similar dimensions, is provisionally associated with *E. liassica*.

Genus *ELATEROPHANES* Handlirsch, 1906

Type species. *Elater vetustus* Brodie 1845, here designated. Lias, U.K.

Diagnosis. Prothorax about as broad as long, with elongate posterior corners.

Discussion. Handlirsch (1906: 436) proposed *Elaterophanes* for two species, both based on specimens from the Lower Lias of Apperley, Gloucestershire, and illustrated by Brodie (1845: pl. vii, figs 1 & 2). Brodie (1845: 10) named one specimen (pl. vii, fig. 1) as *Elater vetustus* but left the second specimen un-named in the family Elateridae. Giebel (1856) named this second specimen *Elater socius*, and Handlirsch transferred both species to *Elaterophanes* (1906: 436). Examination of both Brodie's original specimens indicates that *E. socius* Giebel should be regarded as a junior synonym of *E. vetustus* Brodie. Dolin (1975) mentioned that the systematic position of *Elaterophanes* had not been elucidated. Examination of the type specimen of *E. vetustus* and a study of Dolin's key to the Elateridae (1975: 475) suggests that this genus would fit in the tribe Hypnomorphini. The femoral plates on the hind coxae do not have an extra long side, as in the Desmatini, and the prosternal suture looks closed along its length.

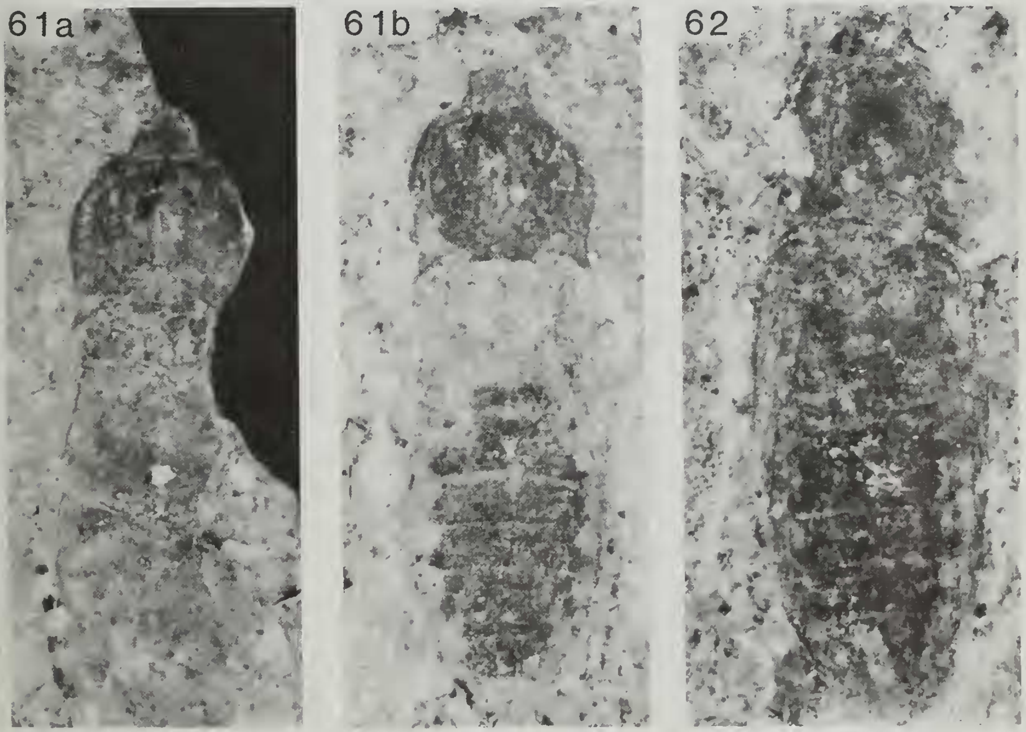
Elaterophanes regius sp. nov.

Figs 61–62

Diagnosis. As genus, but smaller than type species and with lateral thoracic margins curved, not straight.

Name. 'Kingly'.

Description. Head small in proportion to thorax. Prothorax rounded anteriorly. Elytra not visible. Base of coxae visible; peg-like process at base of prothorax and probable cavity faintly



Figs 61–62 *Elaterophanes regius* sp. nov. (Coleoptera). Fig. 61, **holotype,** In.59385, length 7 mm. a, part. b, counterpart. Fig. 62, paratype, In.53952, length 8 mm.

indicated in anterior (ventral) of mesothorax. These structures form part of the peg click-mechanism of the beetle. Abdomen elongate, slightly broader posteriorly. Apex of abdomen with slight swelling indicating female genitalia.

Holotype. In.59385 (Fig. 61); Flatstones, Black Ven, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 7–8 mm body length.

Paratype. In.53952 (Fig. 62); data as type.

Discussion. The general shape of this click-beetle is very similar to Recent species of *Agriotes* Eschscholtz. *E. regius* is smaller than *E. vetustus* (Brodie) (10 mm long) from the Lower Lias, Gloucestershire. The elytra of *E. regius* are probably buried beneath the visible parts of the fossil. The paratype is the larger specimen but otherwise their preservation and proportions are similar except that the eyes are more clearly preserved on the paratype specimen. *Elaterophanes regius* is provisionally placed in the Hypnomorphini but the main diagnostic characters for this tribe are not clear on the fossil.

Family **CUPEDIDAE** Latreille, 1825

Genus ***LIASSOCUPES*** Zeuner, 1962

Type species. *Liassocupes parvus* Zeuner, by original designation (Zeuner 1962: 167). Lower Lias, U.K.

Diagnosis. Cupedid with rounded pronotum (Zeuner 1962).

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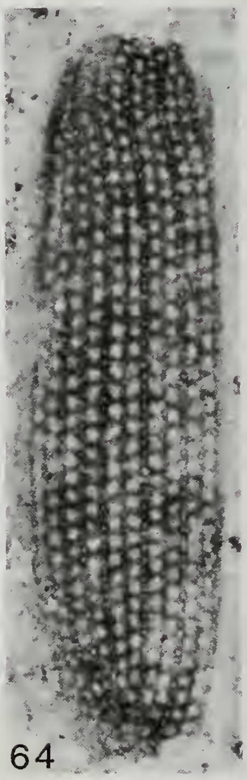

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Figs 63–64 *Liassocupes parvus* Zeuner (Coleoptera). Fig. 63, holotype, In.64008, elytra 4 mm. E = eye, T = thorax; head and thorax rotated, see p. 167. Fig. 64, In.49210, elytron 4·8 mm long.

Liassocupes parvus Zeuner, 1962
Figs 63–64

1962 *Liassocupes parvus* Zeuner: 167, pl. 27, fig. 4.

In the type specimen the head and thorax, if in fact they are part of the same specimen, are rotated at an angle to, and slightly separated from, the elytra (Fig. 63). The actual shape of the thorax is indistinct; it may well have been longer than broad. One new specimen (In.49210, Fig. 64) from the type locality is regarded as conspecific: it is a single complete elytron which clearly shows the typical cupedid pattern. Its width is the same as the incomplete holotype, but it is longer because it is complete.

HOLOTYPE. In.64008 (Fig. 63); Flatstones, Black Ven, Charmouth, Dorset. Jackson colln. Dimensions: Length (incomplete), 4 mm.

OTHER MATERIAL. In.49210 (Fig. 64); data as holotype. Dimensions: Length (complete), 4·8 mm.

Liassocupes (?) *maculatus* sp. nov.
Figs 65–66

DIAGNOSIS. Cupedid with 12 rows of pale spots; whole elytra covered with black spots.

NAME. 'Spotted'.

DESCRIPTION. External margin flattened, broadest towards thorax. Margin clearly with row of paler areas; junction between flattened edge and curved part clearly defined, resembling a subcostal vein. Elytra covered by rounded and equally spaced black spots. Apex of elytra pointed. On counterpart (In.53949, Fig. 66b) the black spots are more concentrated in anterior part. Pale areas slightly broader laterally, clearly demarcated by darker areas between.

HOLOTYPE. In.49577 (Fig. 65); Flatstones, Stonebarrow, Charmouth, Dorset. Jackson colln. Dimensions: Length 12·2 mm, width 3·8 mm.

PARATYPES. In.51038, In.53949 (Fig. 66), In.59133. Same data.

OTHER MATERIAL. In.59361, ? In.59154.

DISCUSSION. This species is only provisionally placed in *Liassocupes*. It has particularly well-marked and distinctive elytra with part and counterpart showing slightly different features. The flattened rim is very sharply demarcated from the curved part and may be marked by a vein; alternatively this appearance may be due to the concentration of black dots along this line. The striae do not show clearly on this species.

Liassocupes (?) *giganteus* sp. nov.
Fig. 67

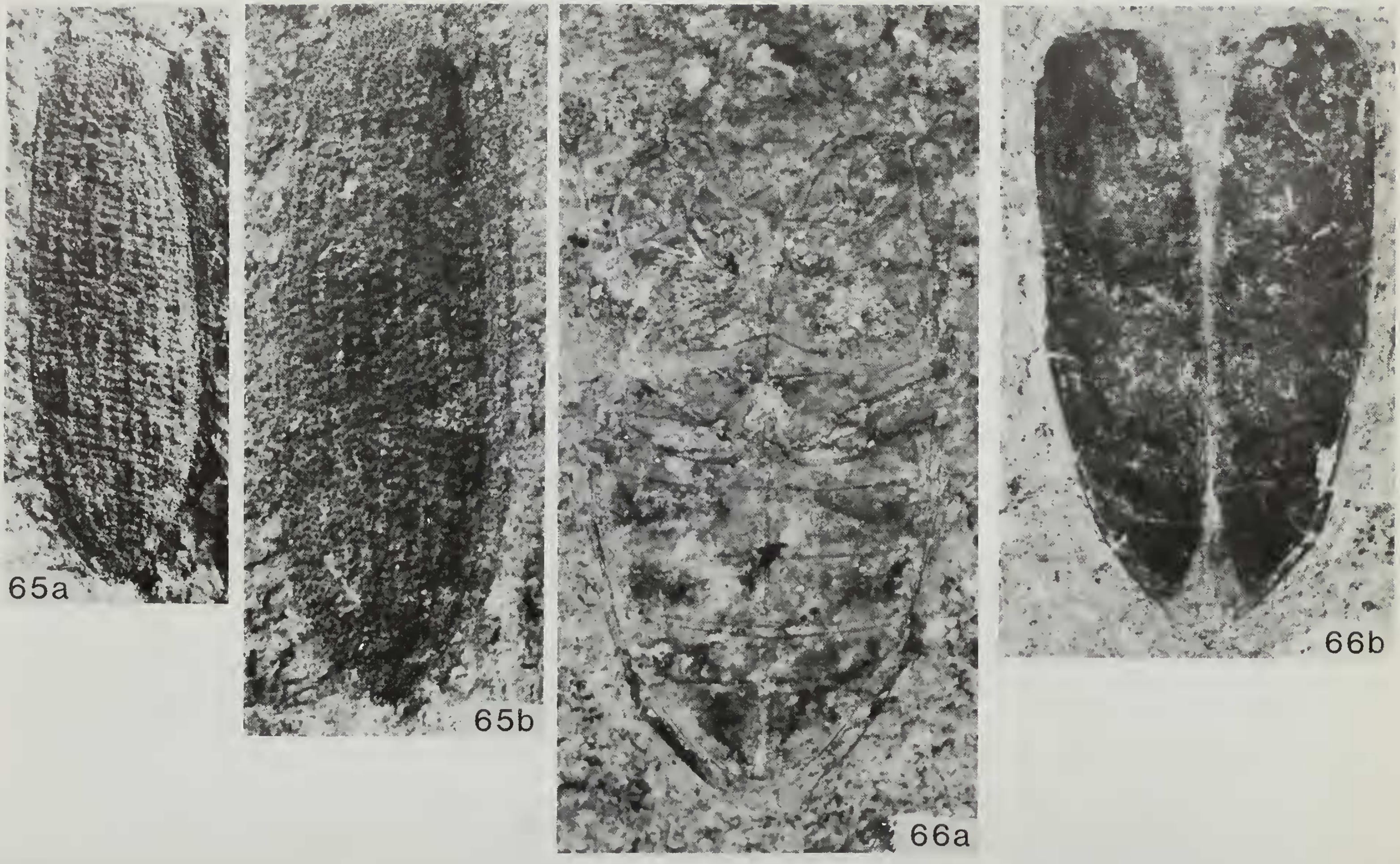
DIAGNOSIS. Elytra with reticulate pattern and scarcely any trace of longitudinal striae.

NAME. 'Giant-like'.

DESCRIPTION. Elytra with pointed apex and rounded anterior margin. Slight lateral flattening along outer margin. Reticulate pattern very distinctive with almost octagonal cells, each with raised central point. Trace of ribbing in subcostal/radial area.

HOLOTYPE. In.51026; Flatstones, Stonebarrow, Charmouth, Dorset; part and counterpart. Jackson colln. Dimensions: 21·4 × 7·8 mm.

DISCUSSION. This is the largest beetle elytron from the Lias. In several characters it resembles species of Taldycupedidae (Rohdendorf 1962) with similar reticulate pattern and obscure ribbing. At present species of this family are known only from the Permian and Upper Trias. *L. giganteus* is only provisionally placed in *Liassocupes* and might well be a late example of Taldycupedidae.



Figs 65–66 *Liassocupes* (?) *maculatus* sp. nov. (Coleoptera). Fig. 65, **holotype,** In.49577, elytron, 12·2 mm long. a, photographed dry. b, photographed wet. Fig. 66, paratype, In.53949. a, part. b, counterpart: fossil has split between elytra and rest of abdomen.

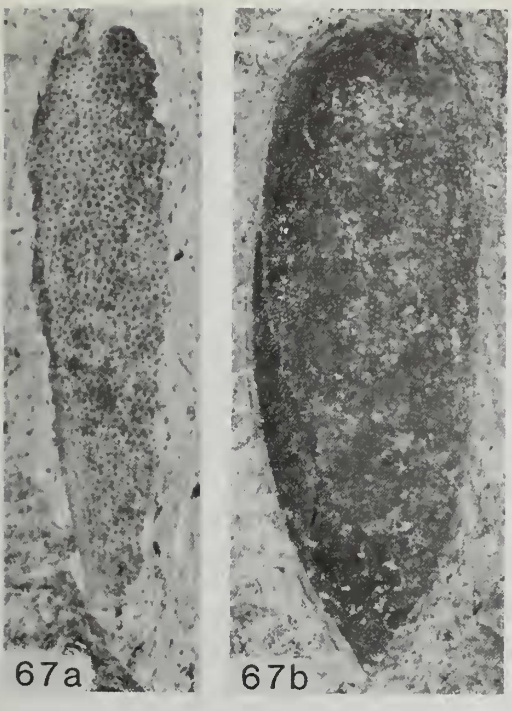


Fig. 67 *Liassocupes* (?) *giganteus* sp. nov. (Coleoptera). **Holotype,** In.51026, 21·4 mm long. a, part. b, counterpart.

Fig. 68 Carabidae (?) species (Coleoptera). In.53923, 11·2 mm long.

Family **CARABIDAE** Latreille, 1825

The following are provisionally placed in this family: In.53923 (Fig. 68); In.51040 (Fig. 69); In.49572 (Fig. 70); In.49222 (Fig. 71).

Superfamily **BYRRHOIDEA**

Provisionally placed in this superfamily: In.64021 (Fig. 72).

Superfamily **DRYOPOIDEA**

Provisionally placed in this superfamily: In.49215, In.49217, In.49218, In.49562, In.51009 (Fig. 74), In.53896, In.53932, In.53950, In.53992, In.59101 (Fig. 73), In.59122, In.59379, In.59398, In.64024 (Fig. 75). Several of these may be species of Psephenidae; many are probably water beetles.

Superfamily **CURCULIONOIDEA**

Provisionally placed in this superfamily: In.59097, In.64022, In.51000.

Curculionidae, gen. et sp. indet.

One specimen (In.64045, Fig. 76) is placed in this extant family of weevils on the basis of the position of its head. This is tucked in under the pronotum with the rostrum lying along the ventral part of the body (Fig. 76). If the species had been prognathous with the rostrum

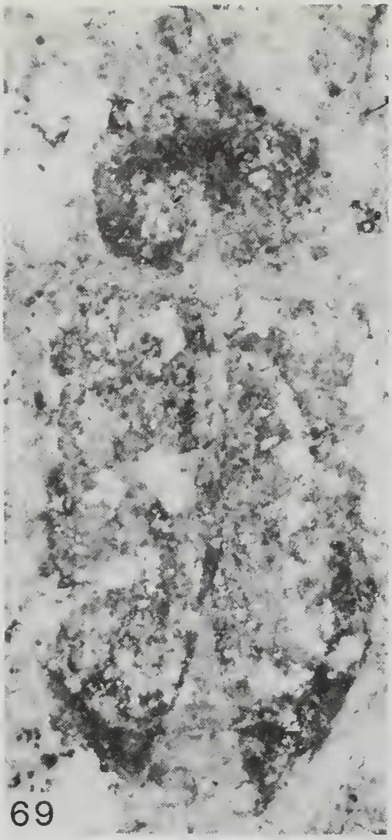

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Fig. 69 Carabidae (?) species (Coleoptera). In.51040, 6·0 mm long.
Fig. 70 Carabidae (?) species (Coleoptera). In.49572, 5·5 mm long.

outstretched then it would have been unlikely to have been preserved with the head and rostrum under the body. On the strength of this it is provisionally placed in the Curculionidae. Although undoubtedly a weevil, few other features can be seen on the specimen which is therefore not classified further. Previously, weevils have been recorded from the Lower Cretaceous and Upper Jurassic (Arnoldi 1977); other Mesozoic weevils from the Upper Jurassic/Lower Cretaceous are described by Whalley & Jarzembowski (1985), but the Dorset specimen, from the Obtusum Zone, is the oldest known example.

COLEOPTERA, *INCERTAE SEDIS*

Family uncertain

There are a further 15 specimens which are fairly distinctive and can be differentiated from the other Coleoptera described but cannot be associated with any Recent family. There are a large number of fossil families, particularly from the Russian Jurassic, with which these have been compared but no satisfactory association can be made. They are separated into 12 species-groups which are considered in the general analysis of the fauna as representing distinct species.

Species 1, In.53967 (Fig. 78).
Species 2, In.59396 (Fig. 77).
Species 3, In.49238, In.49603, In.51020, In.51045.

Fig. 71 Carabidae (?) species (Coleoptera). In.49222, 11·0 mm long.
Fig. 72 Byrrhoidea (?) species (Coleoptera). In.64021, 7 mm long.
Fig. 73 Dryopoidea (?) species (Coleoptera). In.59101, 5 mm long.
Fig. 74 Dryopoidea (?) species (Coleoptera). In.51009, 4·7 mm long.


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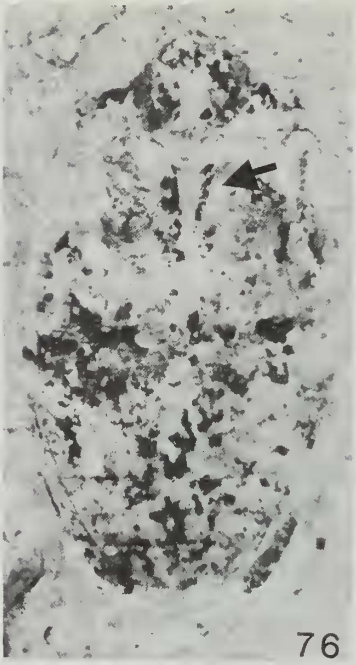
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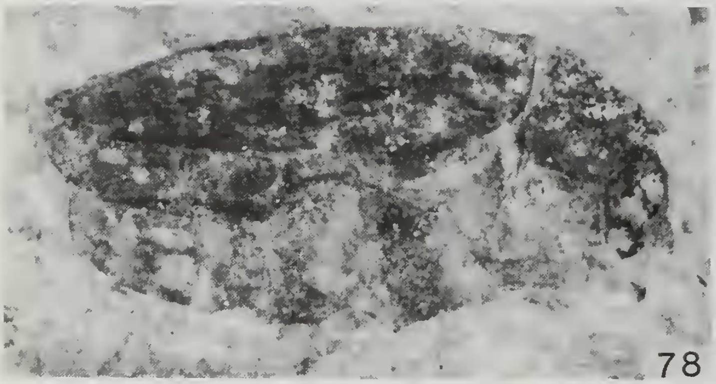
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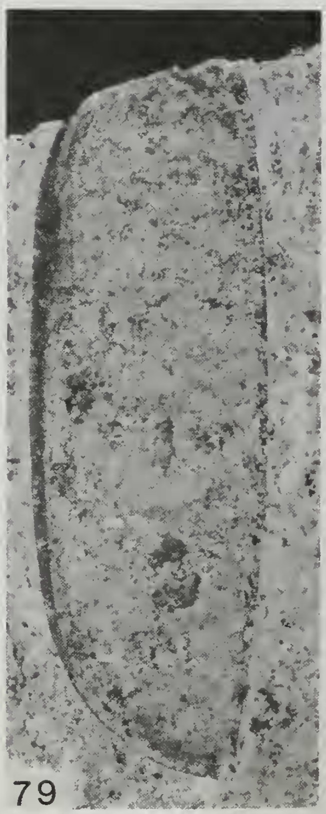
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Fig. 75 Dryopoidea (?) species (Coleoptera). In.64024, 5·5 mm long.

Fig. 76 Curculionidae gen. et sp. indet. (Coleoptera). In.64045, beetle length 5·5 mm. Arrow indicates the rostrum.

Fig. 77 Coleoptera species 2. In.59396, 10 mm long (incomplete).

Fig. 78 Coleoptera species 1. In.53967, 5 mm long. Fossilized in lateral position.

Fig. 79 Coleoptera species 10. In.59362, 14 mm long.

Species 4, In.49571.
Species 5, In.53961.
Species 6, In.49242.
Species 7, In.53977.
Species 8, In.59949.
Species 9, In.59150.
Species 10, In.59362 (Fig. 79).
Species 11, In.59389 (Fig. 80).
Species 12, In.59132, cf. *Omma liassica* Crowson, from the Upper Lias, Warwickshire (Fig. 81).

Family uncertain

The final group of beetles considered are curious, in that while we have many specimens we still do not know their relationship with Recent families.

Zeuner (1962) compared them in general appearance with species of *Tenebrio* (Suborder Polyphaga) or *Feronia* (Suborder Adephaga). Superficially the elytral patterns can be compared with Recent species of *Julodis* Eschscholtz (Suborder Polyphaga, Buprestidae), but *Julodis* species are much larger than the species discussed below. A further suggestion for a Recent family in which they might be included is the Melyridae, where some of the species have ridged elytra (B. Levey, personal communication). However, the pattern of lines on the elytra clearly joins up in the fossils whereas in Melyridae the ridges are separate. Insufficient specimens with the head and thorax have been found to make a reliable assessment of their systematic position but specifically they are very distinct. These beetles are known only from the English Lias and Rhaetic where they are not only conspicuous but relatively abundant.

Genus ***HOLCOPTERA*** Handlirsch, 1906
[= *Holcoelytrum* Handlirsch, 1906]

Type species. *Harpalus schlotheimi* Giebel 1856, by monotypy (Handlirsch 1906: 453). Upper Triassic–Lower Jurassic, U.K.

Handlirsch (1906) erected both *Holcoptera* and *Holcoelytrum*, but Cockerell (1915: 480) synonymized the two names, clearly giving the priority to *Holcoptera*. Zeuner (1962: 167), however, overlooked this, preferring *Holcoelytrum*, which was reasonable on account of the loss of the type specimen of *Holcoptera schlotheimi*. Cockerell's designation and synonymy, however, have priority, and furthermore we now have the neotype for the type species of *Holcoptera* designated by Zeuner (1962).

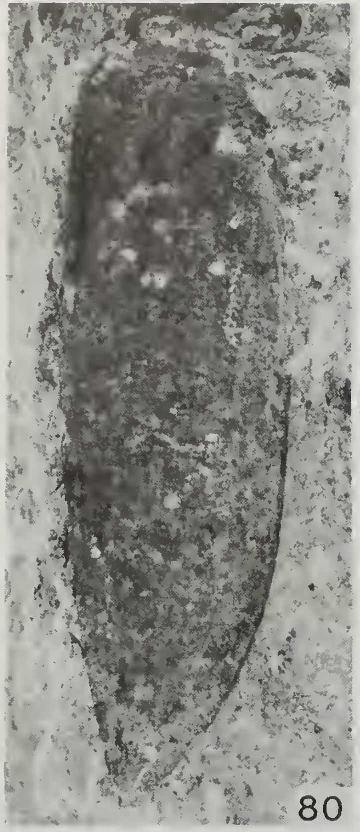
These are very distinctive and strongly patterned beetles, and although fragmentary specimens of the genus are not easily separated into species, the generic identity of even a small piece of a *Holcoptera* is easily recognized. It is possible such fragments could be used as stratigraphic indicators.

Holcoptera schlotheimi (Giebel 1856)
Fig. 82

1845 (Harpalideous Carabidae) Brodie: 101, 124; pl. 6, fig. 28.
1856 *Harpalus schlotheimi* Giebel: 63.
1906 *Holcoptera schlotheimi* (Giebel) Handlirsch: 453; pl. 41, fig. 63.
1915 *Holcoptera schlotheimi* (Giebel); Cockerell: 480.
1962 *Holcoelytrum schlotheimi* (Giebel); Zeuner: 170; pl. 27, fig. 5.

Diagnosis. Elytron over 5 mm long, with four black stripes (Zeuner 1962: 170).

Description. Eyes prominent, head protruding between eyes, rounded in front. Prothorax broader than long, possibly with median suture. Elytra with broad black stripes, possibly remnants of thicker part of elytra. Black stripes usually thinner than white, often with broader, angled part towards anterior end of elytra.



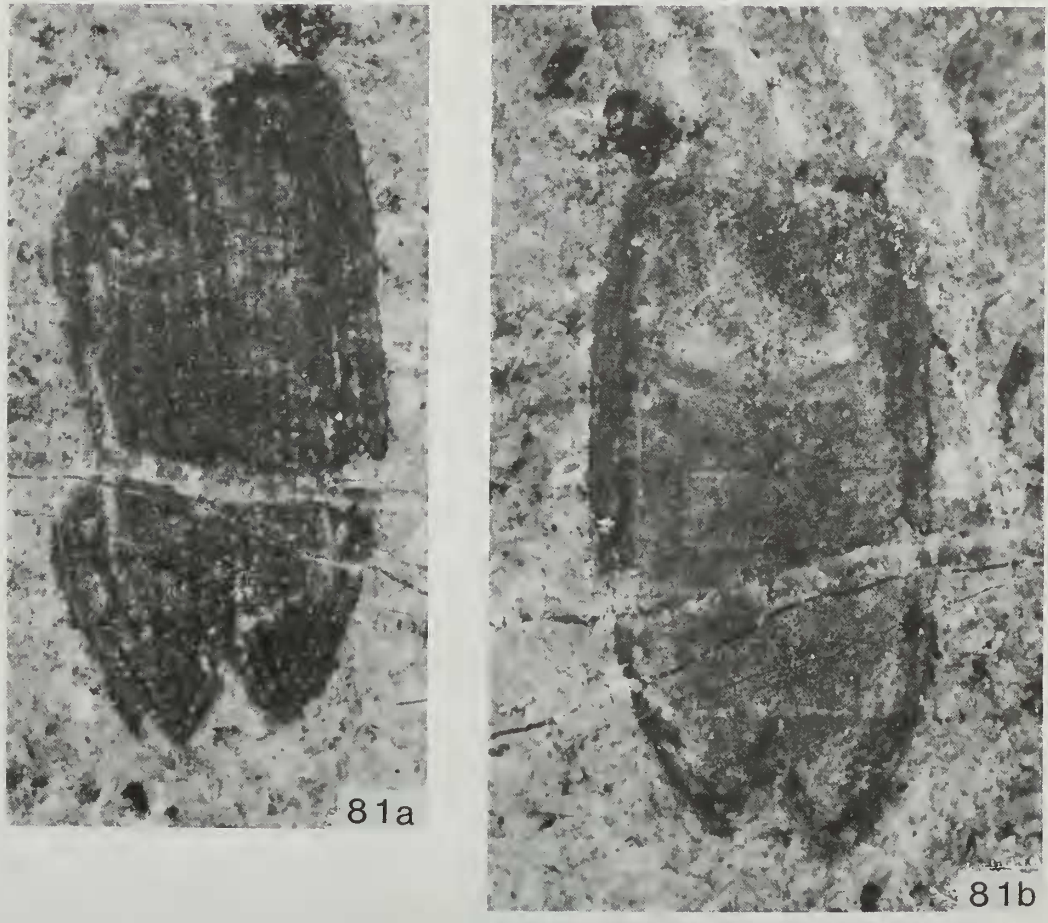


Fig. 80 Coleoptera species 11. In.59389, 20 mm long.

Fig. 81 Coleoptera species 12, cf. *Omma liassica* Crowson. In.59132, 7·7 mm long. Note contrasting preservation of part and counterpart; fossil split between elytra and rest of body. a, part. b, counterpart.

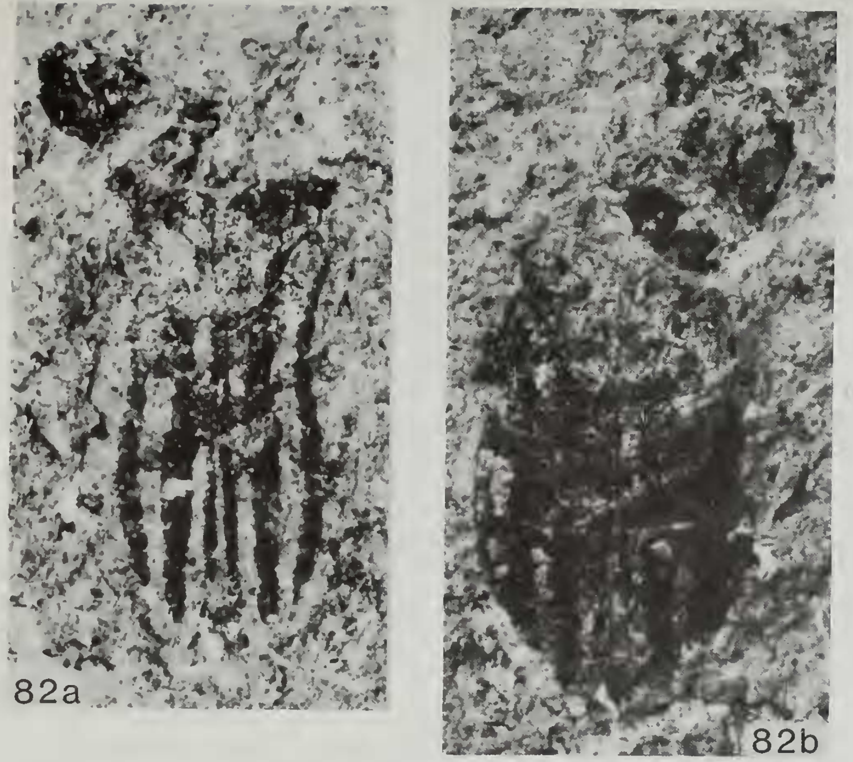


Fig. 82 *Holcoptera schlotheimi* (Giebel) (Coleoptera). In.53990, elytra 5–6 mm, total length of insect 7–8 mm. a, part. b, counterpart. Specimen listed by Zeuner, 1962: 170.

Fig. 83 *Holcoptera giebeli* (Handlirsch) (Coleoptera). In.53937, part, elytra 12 mm long. See Fig. 84.

NEOTYPE. In.59115; Flatstones, Charmouth, Dorset. Jackson colln. Designated by Zeuner, 1962.

ADDITIONAL MATERIAL. Additional to that listed by Zeuner, 1962: In.51019, In.53958, In.59115, all from Dorset. One further specimen, *ex* Brodie colln, locality uncertain, U.K. (probably Aust, near Bristol), in U.S. National Museum, cat. no. 61406. Seven specimens, Aust, near Bristol (Rhaetic), in Yorkshire Museum.

DIMENSIONS. Total length, 7·5–8 mm; elytra 5–6 mm.

DISCUSSION. This species is smaller than *H. giebeli*. It is also much less common, only five specimens being known from Dorset whereas there are 47 specimens of *H. giebeli*. *H. schlotheimi* appears in the Rhaetic in the U.K. and there are more specimens from the Lower Lias of Gloucestershire and Worcestershire. There are a number of Brodie specimens in other museums both in Britain and abroad, and it is possible that Giebel's type specimen may yet be found. It is unfortunate that Zeuner selected as neotype a specimen from Dorset when there are more specimens available from nearer the original type locality and from the same zone as the holotype.

From the similar sized *H. confluens* Cockerell, *H. schlotheimi* can be distinguished by the narrower and more parallel-sided black stripes. Its exact relationship with *H. confluens*, which is known by a few specimens from the English Lias, is not clear.

Holcoptera giebeli (Handlirsch 1906)

Figs 83–87

1845 (Harpalideous Carabidae) Brodie: 101, 124; pl. 10, fig. 2.
1856 *Harpalus schlotheimi* Giebel: 63 (*partim*).
1906 *Holcoelytrum giebeli* Handlirsch: 453; pl. 41, fig. 64.
1915 *Holcoptera giebeli* (Handlirsch) Cockerell: 480.
1962 *Holcoelytrum giebeli* Handlirsch; Zeuner: 168; pl. 27, figs 6–8.

DIAGNOSIS. Elytron over 10 mm long, with five black stripes (Zeuner 1962: 168).

DESCRIPTION. Thorax broad, slightly pointed on posterior margin. Prothorax probably divided. Strongly patterned black and white stripes on elytra, forming complete margin round elytra with central stripes joined posteriorly. Abdomen broad.

HOLOTYPE. I.3581 (Gloucestershire); Brodie colln.

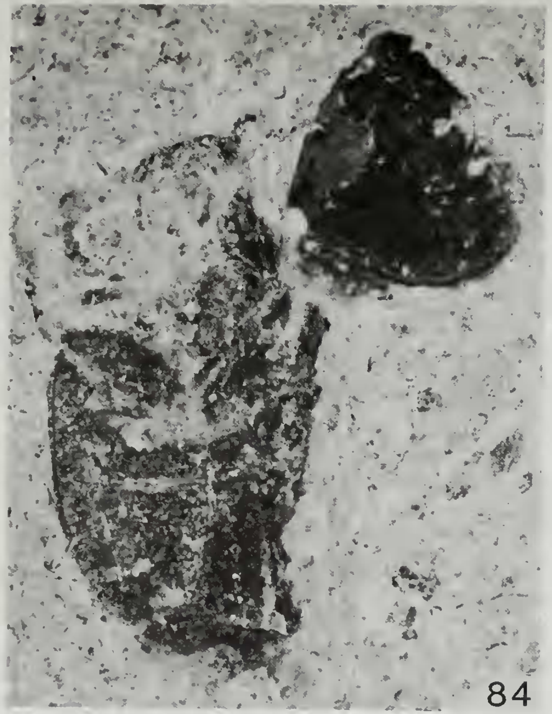
OTHER MATERIAL. Zeuner (1962: 168) listed 43 specimens from the Dorset Lias. There are four additional specimens from the Jackson collection, not listed by Zeuner: In.49618, In.51019, In.53921, In.53927. Also I.10977, Strensham, Worcestershire; Brodie colln (Upper Trias).

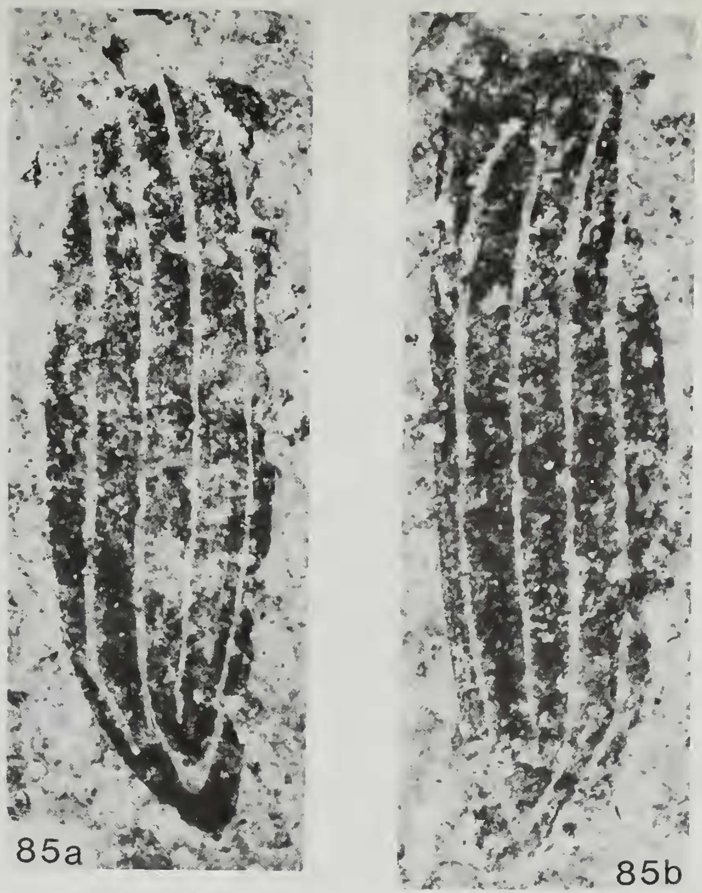
DIMENSIONS. 11·8–14 mm, elytra only.

DISCUSSION. Although there are more specimens of this species in the Dorset Lias than of *H. schlotheimi*, they are all incomplete, lacking the head and in most cases the thorax.

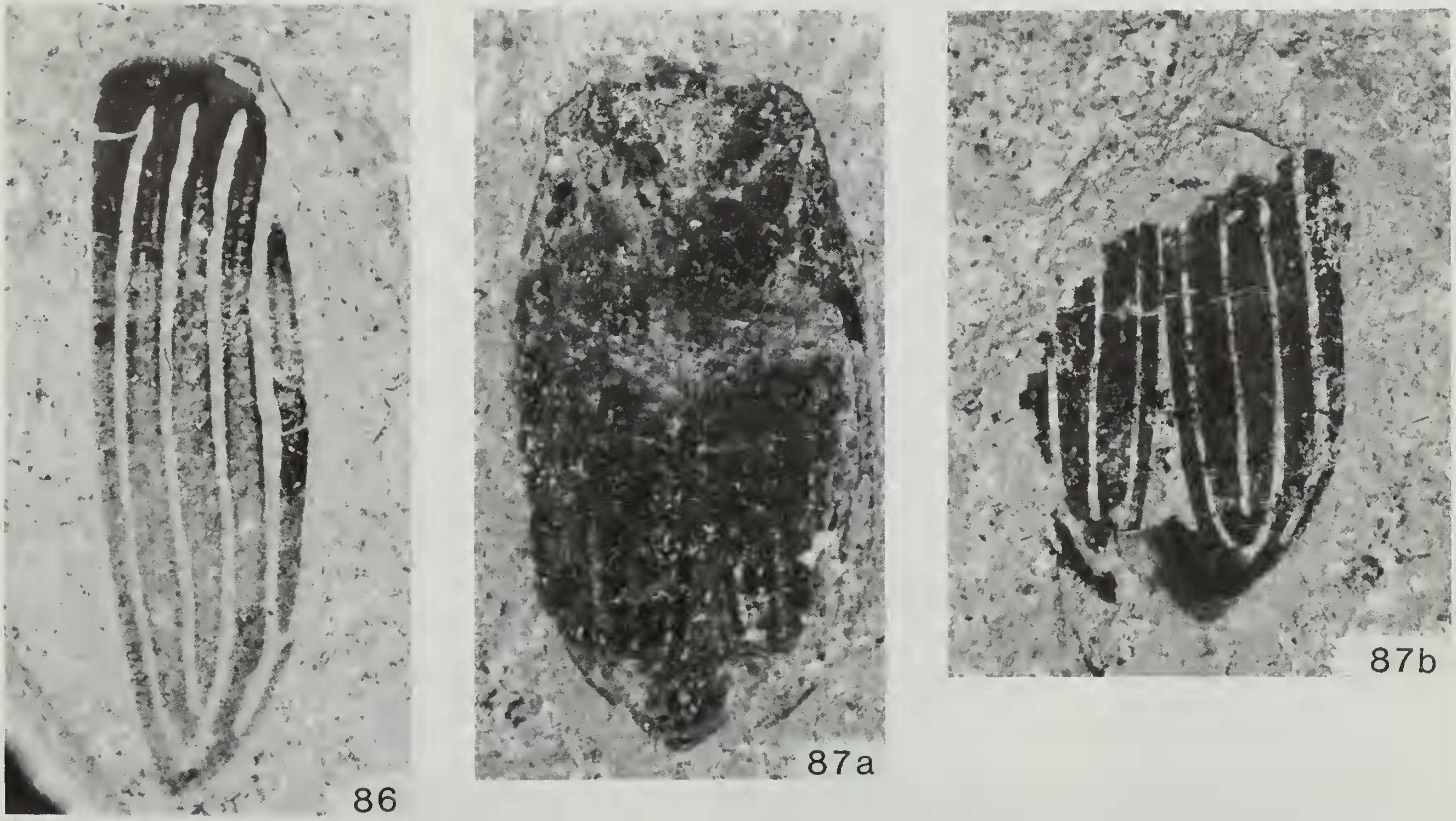
Discussion

Zeuner (1962) drew attention to the similarity he considered was shown by the conditions in Dorset in the Lower Lias and mangrove swamps of present-day tropics. This analogy was based on the absence of wave action and the sedimentation under protected conditions, with the presence of a marine element indicating tidal flow. He also considered that the mixture of marine animals and insects might have indicated that the Jurassic sea was of low salinity in the area. He discussed this concept in some detail with an analysis of various present-day brackish water insect faunas. He considered the deposits could represent a brackish water environment with access to the sea. He suggested that there was evidence for extreme waterlogging of the insects, caused by prolonged drifting and slow sinking: this was demonstrated by the state of the specimens in the deposit, with, for example, the beetles being compressed dorsoventrally





Figs. 84–85 *Holcoptera giebeli* (Handlirsch) (Coleoptera). Fig. 84, In.53937, counterpart, elytra 12 mm long. See Fig. 83. Fig. 85, In.53989, 11 mm long. a, part. b, counterpart.



Figs 86–87 *Holcoptera giebeli* (Handlirsch) (Coleoptera). Fig. 86, In.53981, 13 mm long. Fig. 87, In.53928, 12 mm long. a, part. b, counterpart.

and with wrinkles, indicating that they were wet and decaying when gradually compressed by the sediment. While a few beetles have been found with folds and wrinkles, many are in fact preserved with no dorsoventral flattening or evidence of decay. Some specimens clearly show firm compaction by the calcareous mudstone, but relatively few are distorted by movement of mud, either during or after burial. On the other hand, the twisting or folding of delicate wings is most likely to have occurred when they were very wet and, while the particular examples cited by Zeuner as evidence of waterlogging are not good, there is no doubt not only that the majority of the insects were waterlogged but that some were subject to mechanical disintegration. Curiously at least 40% of the beetles are represented by paired elytra, usually in close proximity or touching. This clearly shows that they must have remained associated until they arrived at the point where they were fossilized. Some of the specimens are not even disarticulated and have limbs attached. All this points to very tranquil deposition in the final stages.

As further evidence of transport and long periods of waterlogging, Zeuner (1962: 159) cited the condition of the dragonfly *Petrophlebia anglicanopsis*, which he said had 'its margins characteristically frayed as in modern insects that have begun to decompose in water'. He figured this specimen (1962: pl. 24, fig. 1) where it can be seen that it is pressed up against an ammonite shell. Removal of the shell (Fig. 8a, p. 123) has shown it is a complete, if slightly crumpled, wing. Very few of the specimens from Dorset in fact look as though they have suffered from prolonged waterlogging and *fraying*; most have remarkably complete margins.

There is nothing in the present study that supports Zeuner's 'mangrove' hypothesis, although there is only negative evidence against it. Few, if any, of the species found would be regarded as characteristic of the specialized 'mangrove' habitat, but there is nothing against the idea that the insects were brought down in the rivers that fed the swamps and then deposited in the more tranquil 'mangrove' conditions. One would, however, have expected more of the 'mangrove' fauna (which in the Lower Jurassic would not have been an angiosperm-type mangrove community) to have been fossilized *in situ* as well. There is no evidence to suggest that the insects were deposited on a tide-line; in fact the extremely fine sediment, gently laminated, would indicate an area of undisturbed mud, certainly not a tide-line. Furthermore the insects are not deposited in concentrations, although a few were fossilized together; mostly they are well separated in separate blocks.

Zeuner stated (1962: 155) that the 'preliminary classification of the specimens . . . has shown that both in composition of the fauna and in the preservation they resemble those of the Lower Lias of Gloucestershire, Warwickshire, and Worcestershire, though there are some significant differences'. The main problem in comparing these two faunas is that the Lower Lias of Gloucestershire and Worcestershire has not been studied critically, except for the Orthoptera, since they were first described. The present study contradicts Zeuner's views strongly and shows that the two faunas were dissimilar, with few species in common, but a critical analysis will have to await a study of the West Country and Midlands Liassic fauna. The insects of the two areas are not the same age: those from the Obtusum Zone of Dorset are stratigraphically younger than those of the West Country, which are mostly Rhaetic or lowermost Liassic (Planorbis Zone). Whalley (1982: 147) briefly compared the two areas, and concluded that their ecological origins were different. Zeuner (1962: 159) discussed the question of the origin of the Dorset fauna. He ruled out the idea that the mud in which the insects had been originally buried had dried out and then been reworked, with the specimens washed out and redeposited, on the grounds that the deposit would then have been in belts of concentrated fragments of vegetation, marine animals and insects. He concluded that this was an area of calcareous mud near land, where insect flotsam was deposited at random in a wave-free, protected environment. He also ruled out that wind could have transported living insects, which then got stuck in the exposed mud. There are very few complete insects which could have landed on mud and been fossilized *in situ*.

Probably the most complete insects are the rather tough waterbugs, some of the Orthoptera and one or two of the rather delicate orthophlebiids. More of the beetles have a few articulated parts but there are a great many isolated elytra. Many of the specimens are represented by a single wing; in a few cases these too are torn or heavily folded. All this indicates mechanical damage to the insects after death. In contrast, in the case of the scale-covered wing of *Archaeolepis* very little mechanical action would be needed to remove the scales which are inserted in sockets in the wing. There are, too, the relatively complete 'sets' of wings, for example the dragonfly (in private hands) or the orthophlebiid (Fig. 47), which cannot have been transported far. There is some evidence that dead insects will float on still water for several weeks (E. A. Jarzembowski, personal communication) and might well be carried some distance before breaking up. The separate parts could then be carried further; for example, individual wings are particularly tough until waterlogged or weakened by fungal or bacterial action, and it is only then that the wing will tear readily—while still unwaterlogged they can resist considerable mechanical damage. There is a difference in the rate of waterlogging, depending on whether the insect was dead and partly dried when it fell in the water or whether it landed in it alive; in the latter case waterlogging and fungal attack are more rapid. Fungal attack usually takes place in fresh water; there is less evidence of its action in salt water. The distance a wing or a whole insect may travel on or in water depends on many factors. Insects with abundant hairs or scales will trap air and may resist wetting for longer after immersion. Assuming an insect avoids being eaten as it is washed along, and this is probably the fate of many that fall into water, it is likely to be damaged more rapidly if it is carried on the water surface where this is broken by wind, waves or the presence of rocks. At certain current speeds, as yet not exactly determined, dead insects *in* a current will not hit large stationary objects (e.g. rocks) as they are swept along below the surface. Thus an entire insect may be gently eased round obstructions by the current flow, where larger objects may be damaged by striking them. Surface tension is also important in the early stages. This may be affected not only by factors already mentioned but also by the nature of the dissolved chemicals in the water, as a degree of natural saponification of debris will materially lower the surface tension and facilitate the wetting of dead insects. Probably the pH of the water, which obviously reflects the chemical content, also affects an insect transported by the current.

Zeuner (1962) was correct in suggesting the Dorset insects were deposited under tranquil conditions. The fine-grained rock is relatively evenly bedded, with little sign of surface disturbance or scourfills, and there is no evidence of concentration of insect fossils other than by obstruction, i.e. where they have been washed up against pieces of wood or an ammonite shell.

Allowing for possible differences in the geographical or ecological origins of the insects in the Dorset fossil assemblage, certain hypotheses can thus be proposed about their origins and the environment from which they were derived. These are listed under three main headings below.

1. **Fresh water**. The aquatic Heteroptera were from non-saline water; this fresh water would also have been needed by the immature stages of all the dragonflies. Although a number of modern dragonflies are migratory and are often found far out at sea, the majority are territorial and do not have a migratory adult phase. Some of the Coleoptera fossils are water beetles and although the adults were probably able to fly they would still have needed fresh water for the immature stages and for much of their adult life. Thus a source of fresh water was needed for some of the insects which, judged from the condition of the specimens, was not far away from the site of fossilization. The fresh water could have been a lake or a river (or both), although it is interesting that no Ephemeroptera or Trichoptera, both of which have aquatic larvae, were found in the fossil assemblage.

One of the belostomatid water bugs (new species 8A, Fig. 42 and p. 146) is in such good condition that it could have flown in; if it was washed in, it is unlikely to have been carried far since there is the minimum of mechanical damage to the insect. There is no sign of fungal damage, which can begin within a week of death in fresh water (E. A. Jarzembowski, personal communication). There was, therefore, a fresh water source for the Dorset Lias—and hence some land—within a few miles, especially since the belostomatids are not noted for long-distance flights.

2. **Marine**. Few insects are truely marine, although a number will tolerate brackish water. Most of the insects in the Dorset fossil assemblage are unlikely to have been dependent on a marine

environment: possibly some of them scavenged on the shore-line but the majority are wholly terrestrial in origin. The environment in which the insects were fossilized is always regarded as completely marine, as evinced by the presence of ammonites. But perhaps ammonites could have been carried into estuaries by tide and wind and have been deposited in a far less saline environment: the modern nautiloid shell will float and certainly gets washed up onto beaches. There is, however, no evidence of a shore line associated with the insect and ammonite fossils and the total absence of fossilized aquatic insect larvae, which are known from other deposits, make it very unlikely that the deposition zone was other than fully marine.

3. **Terrestrial.** There is nothing in the constitution of this particular thanatocoenosis, other than the straight terrestrial/aquatic habitats, to indicate that the insects were *all* derived from the same environment. Certain general facts can be inferred from the species content of the assemblage. The presence of a large and diverse Orthoptera population, with bush-crickets and true crickets predominating, does at least indicate that these were derived from an area where the vegetation was varied; it was more likely to have been an open bush area with trees than the dense shore-line vegetation suggested by Zeuner (1962). The bush-crickets no doubt lived amongst the leafy vegetation of the Filicales which were abundant in the Upper Jurassic (Harris 1961), and these together with the Bennettitales, Cycadales and Coniferales, which have all been recorded from the Lias of Dorset, provided the plants on which the insects lived and fed (Seward 1904). No angiosperms have been reported (Hughes 1976). The presence of numerous dragonflies, apart from indicating non-saline water sources, also suggests that the area from which they were derived was fairly open, rather than densely wooded. Such an abundance of aerial predators also points to an abundant source of food for them. There is no evidence to suggest that the dragonflies were other than predators of flying insects, like Recent species, and there must have been a good source of flying insects which they caught. No doubt many of these were the orthophlebiids which are common in the fossil record, and which, from their appearance and by analogy with present-day Mecoptera, were probably not strong fliers.

Comparison with other Mesozoic faunas

1. **British Mesozoic.** There are extensive insect faunas in the British Lower and Upper Jurassic (e.g. Warwickshire, Worcestershire, Dorset) but none has been recently monographed. Preliminary studies (Whalley 1982, 1983) show that, apart from the relative ages, there are fundamental differences between the Dorset Lower Lias and the others, sufficient to indicate that they were drawn from ecologically different sources.

An initial comparison of the Lower Cretaceous (Wealden) fauna with the Dorset Lias shows that the proportion of extinct families is much higher in the Liassic fauna (E. A. Jarzembowski, personal communication).

2. **Continental Europe and Asian Mesozoic.** The data from two continental European and one Asian fauna were examined and tabulated (Table 2). The Upper Liassic fauna from eastern Lower Saxony was studied by Bode (1953). He described over 300 new species from the collection, recognizing only 15 previously-described species six of which he had described earlier from the same locality in Saxony. The insect fauna was rich in Homoptera but Coleoptera were again the most numerous, although the percentage of beetles in the total fauna was lower than in the Dorset Lias (27·4% Saxony; 39·0% Dorset). The percentage of species of Heteroptera was higher in the Dorset Lias than in the other three faunal assemblages (Table 2) but they had more Neuroptera and Diptera.

Since the Dorset figures in Table 2, apart from other variables, do not represent an exactly contemporary fauna, too much must not be read into the figures. Differences in the assemblages are likely to be caused by a number of factors, the two primary ones being the differences in age (Lower Lias, Upper Lias, Upper Jurassic) and ecological difference in the areas from which the insect fossils were derived. To emphasize the caution needed in considering these figures, the similar percentages for Orthoptera should be examined in more detail. The Dorset Lower Lias has 14% while the Upper Lias (Saxony) site has 15%, but the species composition is quite

Table 2 Percentage of species in each family. Saxony and Dobbertin data from Bode (1953); Karatau data from Rohdendorf (1968).

	Dorset Lower Lias	Saxony Upper Lias	Dobbertin Upper Lias	Karatau Upper Jurassic
Ephemeroptera	—	—	—	0·3
Blattodea	3·1	1·3	0·2	3·4
Orthoptera	14·0	15·0	20·7	2·4
Dermaptera	1·5	—	—	0·6
Odonata	10·9	6·5	6·2	10·0
Plecoptera (*s. l.*)	—	2·2	0·7	—
Heteroptera	14·0	7·3	6·2	4·8
Homoptera	6·2	18·6	21·5	4·5
Psocoptera	—	—	—	0·6
Thysanoptera	—	—	—	0·3
Raphidioptera	3·1	—	—	2·4
Neuroptera	—	6·5	4·6	4·1
Mecoptera	4·6	5·9	9·3	2·4
Trichoptera	—	0·5	8·8	1·0
Lepidoptera	1·5	—	—	—
Diptera	1·5	7·9	11·9	22·5
Coleoptera	39·0	27·4	9·3	21·1
Hymenoptera	—	—	—	18·7

different. In the Dorset Lias the family Gryllidae predominated while in the Saxony fauna it was the Elcanidae.

One of the differences between the faunas is the total absence of Trichoptera, Plecoptera (*sens. lat.*) and insect larvae from the Dorset Lias. This certainly indicates a different ecological source for the faunas. Probably the most striking difference is between the Lower Jurassic (the Liassic faunas) and the Upper Jurassic. The proportion of Diptera has virtually doubled in the Upper Jurassic, while a large number of Hymenoptera have appeared. It is possible to argue that, apart from the age, the appearance of Hymenoptera in the fauna is due to the specialized area from which the assemblage was derived; Hymenoptera have not, however, been found in many Lower Jurassic sites. The high proportion of Diptera and Hymenoptera, and even of Neuroptera, may indicate a derivation of the Upper Lias assemblages from areas more wooded than that of Dorset.

Lin (1976) studied a small Middle/Upper Jurassic fauna from China where the composition of the fauna was broadly similar to the European sites (for example in the absence of the Trichoptera), but there were more Diptera and a smaller proportion of Orthoptera.

Palaeogeography

Although there were four land masses in the Sinemurian which bordered the 'Western Approaches – English Channel' (Ziegler 1982, Naylor & Shannon 1982), only the Cornubian (or Cornish) Massif is considered to be a likely land-source for the insects which fossilized in Dorset. The other land masses, the London–Brabant Massif, Armorican Massif and Welsh High, are considered to have been too far away. In the palaeogeographic maps produced, the Western Approaches Island (Hallam 1975), and the Cornish Platform (Naylor & Shannon 1982) or Cornubian Massif (Ziegler 1982), are not extended as far south-eastwards as suggested by the evidence from the insect fossils.

The ecological (and age) difference which is apparent between the Dorset and Midlands Lias indicates either that these two faunas were derived from different areas, or if they were derived from the same land mass, that the age difference (about 5 million years) had brought about ecological changes. The age difference between the Midlands Lias and Dorset Lias is between the Upper Sinemurian (Obtusum Zone, Dorset) and the Hettangian (Planorbis Zone, Midlands). From the palaeogeographic map of Ziegler (1982) it is possible to consider that the proximity of the Welsh Massif to the Midlands could have provided their fossil assemblage and that the Cornubian (Cornish) Massif provided the Dorset assemblage. As an indication of the different ecological origins of the faunas from the two zones, one of the clearest examples is the orthopterous family Bintoniellidae. This family is abundantly represented in the Lower Lias of the Midlands and occurred in the Lower Sinemurian (Bucklandi Zone), 67 km south of Plymouth (Whalley 1982). The family is absent from Dorset where the Orthoptera are well represented by other families.

The relatively undamaged landbugs (Family nov. 1, p. 143) and almost complete waterbug (new species 8A, p. 146) must have flown in, or only been carried a short distance by currents. The wing of the moth-like *Archaeolepis* (Fig. 58), preserved with scales attached, again indicates the presence of a land source within 50 miles and probably much nearer. Naylor & Shannon (1982: 138) pointed out that occasional deltaic complexes built up in the seas, and, although they were less well developed adjacent to the Cornubian Massif, these must also be considered as possible sources of the fossilized insects.

Two hypotheses are proposed from this study; either the land mass was within 80 km of the present site of Charmouth in the Lower Sinemurian, or the land was near to this site only once, for a period of some 300,000 years in the Sinemurian. In the whole of the succession at Charmouth, the calcareous mudstone and shale in which the fossils have been found is relatively uniform, with evidence of deposition over a long period under fairly tranquil conditions. However, all the insects and the larger pieces of plants are found in only two adjacent strata, the Obtusum Zone and the Turneri Zone (where some of the insects occur in the Birchi nodules). Thus for some reason there was only one period of some 300,000 years when the land was near enough for the insects to be deposited; the only alternative to this is that the deposition currents changed completely. There is no obvious evidence for major changes in condition of deposition of the marine animals, which might suggest a current change in the area. Therefore, either there were massive changes on the land preventing deposition of more insects, or the land itself receded. Even though the insects are only fossilized in the calcareous nodules and have not been found evenly distributed along the various zones, they are still restricted to these particular zones, in spite of there being many more metres of fine, apparently undisturbed sediment.

I favour the hypothesis of a closer proximity of the Cornubian Massif in the Lower Lias and of its proximity being for a relatively brief period. The conditions under which the sediments and remains of the fauna were accumulating in the Charmouth area need to be reconsidered. The sediments were probably laid down in shallow water, not far from land. The presence of marine ammonites and well-preserved insects in the same deposit indicates that tranquil conditions existed at those horizons in which the insects are now found. It is possible that a land area within a few miles and periodic (? tidal) emergence of the seabed would explain the close juxtaposition of the ammonites and insects.

Phylogeny

Most of the phylogenetic implications are discussed in the systematic section and only a few will be enlarged upon here.

With few exceptions the Dorset Liassic insect fauna was more akin to earlier faunas than those of the Lower Cretaceous and represented the first insect stage of the Mesozoic. Insect fossils from the Cretaceous are dissimilar and can often be placed in Recent families (E. A. Jarzembowski, personal communication), whereas the majority of the species from Dorset belong to extinct families. This points to a major change in the insect fauna between the Lower Jurassic and the Lower Cretaceous, at which some modern families appeared. A similar change in the marine faunas at the Toarcian transgression produced a dramatic change in the faunas (Ager 1983), but the species composition of the land flora in the gymnosperms and ferns did not change, although the proportion of the species in the flora probably did (C. R. Hill, personal communication). Changes seem to have really commenced with the very first appearance of the angiosperms. In a few groups of insects with modern representatives that are also found in the Jurassic, like the anisozygopteran dragonflies or the tettigarctid cicadas, there are many Mesozoic species but very few Recent ones: in fact only two living species in both these groups. In others, such as the freshwater Heteroptera, some of the elaterid beetles and the crickets there are few species in the Lower Jurassic but they can be placed in extant families that are now very diversified. We thus have two extremes in the Lower Lias: on the one hand families showing great diversity but which became extinct or very reduced in diversity by the Cretaceous, and on the other families represented by few examples in the Lower Lias but whose increase in diversity began in the Cretaceous and has continued with time. With the belostomatid waterbugs it is easy to appreciate that the ancestors of this group were able to migrate from the Old World to the New World in the Mesozoic before the continents were widely separated. It is interesting that while the waterbugs are the earliest representatives of Recent families, all the landbugs described from Dorset represent extinct families, and exactly the same phenomenon was found by Popov & Wootton (1977) in the Upper Lias of Saxony.

Unless a species was well adapted to its own environment it would not have 'survived' to be fossilized. Many of the Liassic fossils show a high degree of specialization, comparable in many cases with Recent faunas. For example the Jurassic cricket *Regiata scutra* sp. nov. (Fig. 19 and p. 131) had a typical rolled wing tip (at rest) and the highly specialized venation associated with sound production found in Recent crickets. These highly specialized forms died out and were replaced by equally specialized new forms. A considerable environmental and ecological change must have occurred to render the insect fauna of the Lower Jurassic unsuitable for conditions in the Late Jurassic and Cretaceous.

The Dorset Lias gives us a glimpse of a highly specialized and successful insect fauna heading towards this transition from the older and now extinct families, but which includes a few early representatives of Recent families. The subsequent success of the latter can be judged from the abundance and diversity of the Recent insect fauna.

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New taxonomic names and the page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

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